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Frogs of the Genus *Colostethus* (Anura; Dendrobatidae) in the Andes of Northern Peru

By

WILLIAM E. DUELLMAN

Natural History Museum and Biodiversity Research Center
The University of Kansas
Lawrence, Kansas 66045-7561 USA

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ABSTRACT Seventeen species of the dendrobatid frog genus *Colostethus* are recognized in the Andes and adjacent lowlands in northern Peru. Nine of these species have been reported previously from the region and eight are described as new. Tadpoles of eight species are described and illustrated, and growth trajectories of six species of tadpoles are compared. The greatest diversity of *Colostethus* is in humid montane forests in the northern part of the Cordillera Central, where five species occur at elevations above 1600 m; six other species occur at elevations below 1000 m. Two of these also range into the valley of the Río Marañón, where two additional species occur. *Colostethus elachyhistus* is widespread in the Andes in southern Ecuador and in the northern part of the Cordillera Occidental, including the Cordillera de Huancabamba, the higher parts of which are inhabited by *C. sylvaticus*. *Colostethus elachyhistus* and *C. nexipus* are the only species that occur in Ecuador and northern Peru. Seven instances of sympatry reveal slight differences in size between co-occurring species at most of these sites.

Key Words: Anura, Dendrobatidae, *Colostethus*, new species, tadpoles, Andes of northern Peru, taxonomy, biogeography.

RESUMEN Se reconocen diecisiete especies de dendrobátidos del género *Colostethus* en los Andes y tierras bajas adyacentes del norte del Perú. Nueve de estas especies han sido reportadas previamente para la zona y se describen ocho especies nuevas. Los renacuajos de ocho especies son descritos e ilustrados; se compara los patrones de crecimiento de los renacuajos de seis especies. La más alta diversidad de *Colostethus* se encuentra en los bosques húmedos montanos de la región norte de la Cordillera Central, en donde habitan cinco especies por sobre los 1000 m; dos de estas especies también se encuentran en el valle del río Marañón; en el mencionado valle existen dos especies adicionales. *Colostethus elachyhistus* habita en los Andes del sur del Ecuador y en la región norte de la Cordillera Occidental del Perú, incluyendo la Cordillera de Huancabamba, en cuyas partes más altas se encuentra *C. sylvaticus*. *Colostethus elachyhistus* y *C. nexipus* son las únicas especies que se encuentran en el Ecuador y en el norte del Perú. Siete ejemplos de simpatria revelan pequeñas diferencias en el tamaño de especies en la mayoría de los lugares mencionados.

Palabras Clave: Anura, Dendrobatidae, *Colostethus*, nuevas especies, renacuajos, Andes del norte del Perú, taxonomía, biogeografía.

INTRODUCTION

Frogs currently allocated to the genus *Colostethus* are especially speciose in the Andes of Colombia (Ruiz-Carranza et al., 1996; Rivero and Serna, 2000; Grant and Ardila-Robayo, 2002) and Ecuador (Coloma, 1995; Santos et al., 2003). Many fewer species have been reported from the highlands of northern Peru (Rivero, 1991; Duellman and Wild, 1993; Morales and Schulte, 1993; Morales, 1994). Field parties from the Natural History Museum at The University of Kansas worked in the Andes of northern Peru (departamentos de Amazonas, Cajamarca, Piura, and San Martín) in 1970, 1975, 1979, 1989, and 1991. This fieldwork produced more than 400 specimens of *Colostethus* that are deposited in the Natural History Museum at The University of Kansas and in the Museo de Historia Natural at the Universidad Nacional Mayor de San Marcos in Lima, Peru. In addition to these specimens, additional material was collected by: Kenneth E. Campbell in 1970 and deposited in the Florida State Museum; Richard Thomas and others in the 1970s and deposited in the Museum of Natural Science at Louisiana State University (some specimens transferred to The University of Kansas); Russell A. Mittermeier in 1978 and deposited in the Museum of Comparative Zoology at Harvard University; and Rainer Schulte, a resident of Tarapoto, Peru, in the 1980s and deposited in the Museo de Historia Natural in Lima.

The first species of *Colostethus* recorded from northern Peru was "*Phyllobates*" *sylvaticus* collected by G. K. Noble in 1916 and described by Barbour and Noble (1920). From that inauspicious beginning, more than seven decades passed before Rivero (1991) described *Colostethus idiomelus* and *C. mittermeieri* from Venceremos on the eastern slope of the northern part of the Cordillera Central and *C. poecilonotus* from the Río Marañón Valley. The principal Peruvian researcher on *Colostethus*, Víctor R. Morales, described *C. uticubambensis* and *C. argyrogastrus* from the northern Cordillera Central, and middle Río Marañón valley, respectively (Morales 1994; Morales and Schulte, 1993). In a revision of the *Colostethus trilineatus* Group, Morales (2002) named *C. ornatus* from the Tarapoto region at the eastern base of the Cordillera Central. The range of one Ecuadorian species, *C. elachyhiustus*, was extended into the Cordillera de Huancabamba in Peru by Duellman and Wild (1993); another species described from Ecuador, *C. nexipus*, was reported from Peru by Coloma (1995). Thus, to date, nine species of *Colostethus* have been reported from the Andean region of northern Peru.

The extensive collections from northern Peru include eight new species described herein and the first Peruvian records of another species previously known only from Ecuador. The purposes of this paper are to describe the new species and to review the species of *Colostethus* known to occur in the Andes and associated mountain ranges, intervening valleys, and the immediately adjacent Amazonian lowlands in northern Peru (departamentos of Amazonas, Cajamarca, Piura, and San Martín). Despite the large number of specimens now known from the region, our knowledge of the anurans in the Andes of northern Peru is far from complete. More thorough collecting certainly will extend the known ranges of many species, and the exploration of previously uncollected valleys and mountain slopes surely will reveal additional species, as is evident by the discoveries in other taxa (e.g., Centrolenidae by Duellman and Schulte, 1993, and *Eleutherodactylus* by Duellman and Pramuk, 1999).

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MATERIALS AND METHODS

Specimens in museum collections are identified by their catalogue numbers preceded by the following codes: BMNH = British Museum (Natural History); KU = Natural History Museum, University of Kansas; LSUMNS = Museum of Natural Sciences, Louisiana State University; MHNSM = Museo de Historia Natural, Universidad Nacional Mayor de San Marcos; MCZ = Museum of Comparative Zoology, Harvard University; NHMG = Naturhistoriska Museet Göteborg; UF = Florida Natural History Museum. All specimens from northern Peru and southern Ecuador that have been studied are listed in Appendix 1. Localities from which specimens have been examined are listed with their geographic coordinates, elevation, and vegetation type in Appendix 2. Geographic coordinates were obtained from maps, principally the Mapa Físico Político 1:1,000,000 (1973) but also the Carta Nacional del Perú, 1:100,000 (1986) for those regions so mapped; the Instituto Geográfico Militar, Lima, Peru, produced both sets of maps.

ANDES OF NORTHERN PERU

The geological history, physiography, climate, and vegetation of the northern Andes were described by Duellman and Pramuk (1999); thus, only a thumbnail sketch is presented here. A major orogenic difference between the northern and southern Andes is the deflection in a region of complex interdigitation of relatively low ranges, basins, and valleys—the Huancabamba Depression encompassing the Ecuador-Peruvian border (Figs. 1 and 2). In this region, major rivers flow north or south between intervening north-south highlands. The backbone of the Andes in Peru is the Cordillera Occidental, which north of the Nudo de Pasco in central Peru is separated from the Cordillera Central by the valley of the Río Marañón; this cordillera has its northern terminus at about 5°S latitude and is separated from the Cordillera Oriental by the valley of the Río Huallaga, which turns eastward and forms the northern edge of the Cordillera Oriental at about 7°S latitude.

Nine types of vegetation can be recognized by simplifying the system used by Tosi (1960), as follows.

Desert scrub.—Dry Pacific lowlands receiving less than 150 mm of rain annually with legumes and cacti near the western base of the Andes up to as much as 500 m.

Thorn forest.—A forest dominated by legumes, cacti, and other drought-resistant trees in areas receiving less than 500 mm of rain annually on the western slopes of the Cordillera Occidental to about 1200 m and in the interior valleys of the ríos Chamaya, Chichipe, Huancabamba, Marañón, and Utcubamba.

Measurements, definitions of coloration and structural characters, and numbered characteristics in diagnoses follow those of Duellman and Simmons (1988) with the addition of testes color (Coloma, 1995) and the median lingual process (Grant et al., 1997). Measurements were taken with dial calipers to the nearest 0.1 mm. If sex and reproductive condition were not evident externally (swollen Finger III or vocal sacs in males; eggs visible through body wall in females) sex was determined by dissection. Males with granular testes were determined to be adults; females with expanded, convoluted oviducts or large ova were considered to be adults. Throughout, snout-vent length is abbreviated SVL, and larval labial tooth row formula is abbreviated LTRF. Tadpoles were staged according to Gosner's (1960) table; terminology for tadpoles was based in Altig and McDiarmid (1999). Neuromasts were not evident in any of the tadpoles under 20× magnification; therefore, lateral line systems are not included in the descriptions of tadpoles.

Dry forest.—In areas receiving 1000–2000 mm of rain annually, this forest develops peripheral to thorn forest and in the rain shadows at elevations of 250–600 m of the Río Mayo and middle Río Huallaga.

Montane dry forest.—Isolated patches of this forest exist at elevations of principally at 2000–2500 m in the upper Río Marañón Valley, in the Cordillera Occidental and Cordillera Central.

Humid montane forest.—This is the dominant type of forest on the lower slopes (up to about 2500 m) of the Cordillera de Huancabamba and Cordillera Colán.

Very humid montane forest.—This is the so-called cloud forest characteristic of elevations of 2500–3000 m on windward slopes of the Andes that receive 1000–2000 mm of rain annually. This type of forest occurs at high elevations of the Cordillera de Huancabamba and Cordillera Colán, and the eastern slopes of the Cordillera Central.

Humid subtropical forest.—Forest receiving 1000–3000 mm of rain annually at elevations of 500–1900 m; this is characteristic of the eastern slopes of the Cordillera Central and middle Río Mayo Valley.

Subtropical pluvial forest.—In northern Peru, this type of forest, which receives rainfall in excess of 4000 mm annually, is known only from the crest (> 3000 m) of the Cordillera Central west of the Río Mayo.

Humid tropical forest.—The Amazonian rainforest at elevations \leq 300 m receiving rainfall in excess of 2000 mm annually; great species diversity of trees, some of which form a complete, or nearly so, canopy 30–40 m above the ground.

SUMMARY OF TAXONOMIC CHARACTERS

Compared to their colorful allies (*Allobates*, *Cryptophyllobates*, *Dendrobates*, *Epipedobates*, *Minyobates*, and *Phyllobates*), frogs of the genus *Colostethus* are rather drab in appearance. Living individuals of most species have distinctive colorations, but individuals that were easily distinguished in life commonly are difficult to distinguish once they have been preserved. Consequently, taxonomic studies necessitate detailed and comparable diagnoses and descriptions.

Edwards (1971) made the first attempt to standardize diagnostic character states in *Colostethus* by recognizing 21 features in adults and larvae. Duellman and Simmons (1988) reduced the number to 15 characters of adults. This scheme was partially followed by Morales (1994, 2002) and modified slightly by Coloma (1995) with the addition of testes color; Grant et al. (1997) added the presence or absence of a median lingual process to the diagnostic characters of *Colostethus*, and Grant and Castro (1998) and Grant and Ardila-Robayo (2002) added the so-called black arm band, characteristic of the *Colostethus ramosi* Group. Lötters et al. (2003) added cloacal tubercles and cloacal sheath to their diagnosis. Herein, I define 17 diagnostic features.

1. Size and proportions.—Snout–vent length (SVL) is the straight-line distance from the tip of the snout to the posterior terminus of the body. In making comparisons, I use some subjective terms—small (< 20 mm), moderately small (20–25 mm), and moderately large (> 25 mm). Head length is the chord of head length, i.e., the distance from the tip of the snout to the posterior edge of the articulation of the jaw. Head width is the greatest width of the head. The eye and tympanum sizes are horizontal measurements of the eye and visible part of the tympanum, respectively, and the eye–nostril distance is measured from the anterior corner of the orbit to the posterior edge of the nostril opening. Tibia length is the distance from the knee to the distal end of the tibia. Foot length is the distance from the proximal edge of the inner metatarsal tubercle to the tip of Toe IV.

Snout–vent lengths vary from less than 18.0 mm in males of *Colostethus argyrogaster*, *elachylistus*, *insulatus*, and *ornatus* to 30.0 mm or more in *C. sordidatus* and *C. sylvaticus*. The latter two species and *C. aeruginosus* and *C. utubambensis* have the greatest sexual dimorphism in SVL (Table 1). Proportions are much the same in all species of *Colostethus* in northern Peru. The ratio of head length to SVL is slightly more than the ratio of head width to SVL in most species, but the ratios are reversed in *C. aeruginosus* and are equal in *C. insulatus* and *C. sordidatus*.

The length of the snout is expressed as the ratio of the eye–nostril distance to the length of the eye. Ratios are less than 60% in three short-snouted species (*C. elachylistus*,

Table 1. Body sizes (SVL in mm) of *Colostethus* in the Andes of northern Peru. Values include range (mean, sample size); SexD = sexual dimorphism.

Species	Males	Females	SexD
<i>C. aeruginosus</i>	22.1–25.0 (23.0, 5)	29.2	1.27
<i>C. argyrogaster</i>	17.5–19.8 (18.7, 2)	19.0–22.1 (20.4, 3)	1.09
<i>C. craspedocephalus</i>	19.1	18.5–20.5 (19.7, 5)	1.01
<i>C. elachylistus</i>	15.2–20.9 (17.7, 43)	17.2–23.6 (20.7, 53)	1.17
<i>C. eleutherodactylus</i>	21.0	22.7	1.08
<i>C. idiomelus</i>	19.5–24.8 (22.0, 38)	23.0–27.8 (25.1, 23)	1.14
<i>C. insulatus</i>	17.2–22.0 (19.7, 9)	20.2–26.0 (22.8, 22)	1.16
<i>C. leucophaeus</i>	24.7–25.2 (25.0, 3)	26.1	1.04
<i>C. mittermeieri</i>	27.2	28.2	1.04
<i>C. nexipus</i>	18.6–20.5 (19.3, 10)	20.0–23.1 (21.4, 11)	1.11
<i>C. ornatus</i>	15.7–16.9 (16.3, 2)	15.5–18.4 (17.0, 2)	1.04
<i>C. pulcherrimus</i>	28.2	26.4–29.7 (28.2, 4)	1.00
<i>C. poecilonotus</i>	19.7	20.8–25.2 (22.9, 3)	1.16
<i>C. sordidatus</i>	24.2–29.9 (25.7, 8)	31.8–36.1 (33.6, 3)	1.31
<i>C. spilotogaster</i>	—	24.0	—

ornatus, and *spilotogaster*), more than 70% in four long-snouted species (*C. aeruginosus*, *craspedocephalus*, *idiomelus*, and *sordidatus*), and 60–70% in the other species. The ratio of the length of the tympanum to the length of the eye is less than 50% in five species (*C. leucophaeus*, *mittermeieri*, *nexipus*, *sordidatus*, and *utubambensis*), more than 60% in two species (*C. idiomelus* and *C. pulcherrimus*), more than 78% in *C. spilotogaster*, and 50–60% in the other species. Tibia length is proportionally slightly greater than foot length in most species, but the ratio of each to SVL is essentially the same in *C. poecilonotus*, and foot length is proportionately more than tibia length in *C. leucophaeus*, *pulcherrimus*, and *sylvaticus*.

In the species accounts, I describe the limbs in general, subjective terms that are used in comparison with other species in the region. Thus, the forearm (elbow to wrist) is described as long, slender, or robust. The hind limb is described as short, long, robust, or slender; unless specified otherwise this pertains to the thigh and shank.

2. Disc on Finger III.—In most species of *Colostethus* in the Andes of northern Peru, the terminal discs on the fingers, exclusive of the thumb (Finger I) are expanded to be 1.5–2.0 times the width of the preceding (antepenultimate) segment of the digit (Fig. 3). The discs are barely wider than the preceding segment in *C. elachylistus*, *pulcherrimus*, and *sylvaticus*, and not expanded in *C. idiomelus* (Table 2). Standard comparison is made on Finger III.

3. Relative lengths of Fingers I and II.—When the Fingers I and II are adpressed, Finger I (thumb) is shorter than Finger II in *Colostethus nexipus* and longer than Finger II in



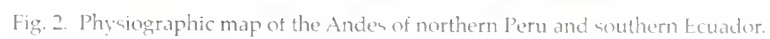


Table 2. States of structural characters and coloration in *Colostethus* from the Andes of northern Peru.

Species	Finger lengths	Disc Width	Lateral fringes	Inner tarsal fold	Toe webbing	Lateral stripes		
						Dorso-	Oblique	Ventro-
<i>C. aeruginosus</i>	I > II	1.5X	Yes	Distal ½	—	No	No	No
<i>C. argyrogaster</i>	I > II	1.5X	No	Weak	Basal III-IV	No	Yes	Yes
<i>C. craspedocephs</i>	I > II	1.5X	No	—	—	No	Diffuse	No
<i>C. elachyhistus</i>	I = II	1.1X	Yes	Distal ½	¼	No	Yes	No
<i>C. eleutherodactylus</i>	I = II	2.0X	No	Distal ½	—	Yes	Yes	No
<i>C. idiomelus</i>	I = II	Not	Yes	Distal ½	—	Yes	No	No
<i>C. insulatus</i>	I > II	1.5 X	Yes	Distal ½	Basal	No	Yes	No
<i>C. leucophaeus</i>	I > II	1.1 X	Yes	Distal ½	½	No	Groin	No
<i>C. mittermeieri</i>	I = II	1.5X	Yes	Distal ½	¼	No	No	No
<i>C. nexipus</i>	I < II	1.5X	Yes	Weak	½	Yes	Yes	No
<i>C. ornatus</i>	I > II	1.5X	No	—	Basal	Yes	No	Yes
<i>C. poecilonotus</i>	I = II	1.2X	No	Distal ½	—	No	Short	No
<i>C. pulcherrimus</i>	I > II	1.1X	Yes	Distal ½	—	No	Yes	No
<i>C. sordidatus</i>	I = II	2.0X	Yes	Distal ¾	¾	No	Yes	No
<i>C. spilotogaster</i>	I = II	1.5X	Yes	Distal ½	Basal	Yes	No	No
<i>C. sylvaticus</i>	I = II	1.1X	Yes	Weak	—	Yes	No	No
<i>C. utubambensis</i>	I > II	1.2X	No	Distal ½	Basal	Yes	Yes	No

C. aeruginosus, *argyrogaster*, *craspedocephs*, *insulatus*, *leucophaeus*, *ornatus*, *pulcherrimus*, and *utubambensis*. Fingers I and II are about equal in length in the other species (Table 2).

4. Fringes on fingers.—The fingers of *Colostethus* never have more than basal webbing, but many species (e.g., *C. aeruginosus*, *elachyhistus*, *idiomelus*, *insulatus*, *leucophaeus*, *nexipus*, *pulcherrimus*, *sordidatus*, *spilotogaster*, and *sylvaticus*) usually have fringes on the inner (preaxial) edges of Finger IV and both sides of Finger II and III. The other species in northern Peru lack fringes (Table 2). The degree of development of fringes is variable; therefore, the standard comparison is made on Finger III. The fringes are broad and conspicuous in *C. aeruginosus* and *C. leucophaeus*, rather thick and keel-like in *C. idiomelus*, and narrow in other species that have fringes. Nearly all of the specimens treated herein were preserved in the same manner, so states of fringes can be compared with relative ease; however, slight desiccation can result in fringes appearing more extensive than in properly prepared specimens.

5. Disc on Toe IV.—The variation in expansion of the terminal discs on the toes approximates that on the fingers (Character 2). Standard comparison is made on Toe IV. In three species (*Colostethus craspedocephs*, *elachyhistus*, and *idiomelus*), the toe discs are slightly more expanded than the finger discs.

6. Fringes on toes.—The presence, absence, and nature of lateral fringes on the toes parallel the condition of the fringes on the fingers (Character 4). Standard comparison is made on Toe IV.

7. Tarsal folds and tubercles.—Of the species of *Colostethus* in the Andes of northern Peru, only *C. eleutherodactylus* has a noticeable outer tarsal fold (= metatarsal fold sensu Grant and Rodríguez, 2001) that extends the full

length of the tarsus; a weak outer tarsal fold is present in some individuals of *C. elachyhistus*. Except for *C. craspedocephs* and *C. ornatus*, all species in the region have an inner tarsal fold. This fold is sigmoid on more or less the distal half of the tarsus; the fold is weak in *C. argyrogaster* and *C. elachyhistus*, and it is flaplike in *C. aeruginosus* and *C. pulcherrimus*. The inner tarsal fold is contiguous with the inner metatarsal tubercle and extends to a tubercle at about the midlength of the tarsus in five species; the tarsal tubercle is small in *C. argyrogaster*, *insulatus*, and *utubambensis*, and it is much larger in *C. eleutherodactylus*. Two species that lack an inner tarsal fold have tarsal tubercles; the tubercle is small in *C. craspedocephs* and elongate and curved in *C. ornatus*.

8. Toe webbing.—The toes are webbed basally in *Colostethus argyrogaster*, *insulatus*, *ornatus*, and *utubambensis*. In two species (*C. elachyhistus* and *C. mittermeieri*), the toes are about one-fourth webbed; they are about one-half webbed in *C. leucophaeus* and *C. nexipus*, and about three-fourths webbed in *C. sordidatus*. Other species of *Colostethus* in the region lack webbing between the toes (Table 2). In the individual accounts of those species having more than basal webbing, the webbing is described following the protocol of Savage and Heyer (1967) as modified by Myers and Duellman (1982).

9–11. Pale longitudinal stripes.—The color patterns of most species of *Colostethus* include one or more kinds of pale stripes; the combinations of these stripes are helpful in identifying species (Table 2). The stripes usually are pale tan or cream, but they are orange-red in *C. nexipus*. Two species in the northern Andes, *C. aeruginosus* and *C. mittermeieri*, lack longitudinal stripes. The dorsolateral stripe (Character 9) extends from at least the occiput to the posterior end of the body above the insertion of the

hind limb; in most species, the stripe is continuous anteriorly along the outer edge of the upper eyelid and along the canthus rostralis to the tip of the snout. Dorsolateral stripes are present in only six species in the region (*C. eleutherodactylus*, *nexipus*, *ornatus*, *spilotogaster*, *sylvaticus* and *utcubambensis*). The oblique lateral stripe (Character 10) is present on the flank in many species; it originates in the groin (at about midheight of the insertion of the hind limb) and may extend anteriorly to the midflank region or even to the posterior edge of the upper eyelid. An oblique lateral stripe is absent in *C. ornatus* and *C. sylvaticus*. The stripe is short and confined to the groin in *C. leucophaeus* and *C. poecilonotus*; it is diffuse in *C. craspedocephalus* and is fragmented in *C. eleutherodactylus* and some individuals of *C. nexipus*. In some species, a pale ventrolateral stripe (Character 11) is present; this is most noticeable in species having a dark venter. Among the species in the Andes of northern Peru, a ventrolateral stripe is present only in *C. argyrogaster* and *C. ornatus*.

12. Coloration of the gular-chest region.—Uniform coloration of the gular-chest region characterizes adults of seven species of *Colostethus* in the Andes of northern Peru—cream in *C. argyrogaster*, *eleutherodactylus*, *leucophaeus*, *nexipus*, *poecilonotus*; pale gray in *C. utcubambensis*, grayish brown or cream in *C. craspedocephalus*, and gray or white in *C. ornatus*. The most common markings in the gular-chest region are a pair of dark brown to black spots posterolaterally on the throat; these are present in adults of *C. elachyhistus*, *idiomelus*, *insulatus*, *mittermeieri*, and present or not in *C. sylvaticus*. Other color patterns on the gular-chest region consist of cream spots on a brown background (*C. aeruginosus* and *C. pulcherrimus*), many small brown spots (*C. spilotogaster*), or a dark gray intrusion laterally on the throat in *C. sordidatus* (may be an incipient pair of dark spots).

13. Coloration of abdomen.—In life, the entire abdominal region is pale cream to creamy yellow or white in most species of *Colostethus* in the Andes of northern Peru, but it is silver in *C. argyrogaster* and gray or white in *C. sordidatus*. Other species have distinctive patterns on the abdomen—mottled gray and white anteriorly and yellow posteriorly on abdomen and ventral surfaces of hind limbs (*C. idiomelus* and *C. sordidatus*), mottled throughout with gray (*C. aeruginosus*), gray with white spots (males of *C. utcubambensis* and some males of *C. elachyhistus*), mottled with gray anteriorly (*C. mittermeieri*), or cream with brown mottling (*C. pulcherrimus*) or spots (*C. spilotogaster*).

14. Sexual dimorphism in coloration.—As is evident from the character states in Characters 12 and 13, sexual dimorphism in coloration of preserved specimens is evident in five species of *Colostethus* in the Andes of northern Peru. Sexual dimorphism in ventral coloration occurs in

four species—gray throat or abdomen in males and cream or white in females (*C. ornatus*, *sordidatus*, and *utcubambensis*), or gray with cream spots in some females versus cream in males (*C. elachyhistus*). The males of *Colostethus argyrogaster* are distinctive in having an orange inguinal region in life.

15. Median lingual process.—The presence of a median lingual process on the dorsal surface of the tongue was reported in nine species of *Colostethus* from Chocóan Ecuador and Colombia, Guyanan Venezuela, and Amazonian Brazil (Grant et al., 1997; Grant and Rodríguez, 2001; Myers and Donnelly, 1997). No species from Peru is known to possess this structure.

16. Swollen fingers in males.—The preaxial part Finger III is swollen laterally in males of many species of *Colostethus*, especially in members of the *Colostethus trilineatus* Group (Morales, 2002). Finger II also is swollen in some males of *C. trilineatus* (Grant and Rodríguez, 2001), and in several other species, e.g., *C. inguinalis* (Grant, 2004) and *C. nubicola* (Ibáñez and Smith, 1995). The only species with a swollen Finger III in the region under consideration is *C. ornatus*, a member of the *Colostethus trilineatus* Group (sensu Morales, 2002).

17. Testis color.—Coloma (1995) noted that the testes are brown in three species of *Colostethus* in Ecuador. All male *Colostethus* examined from Peru have white testes, as do most species in Ecuador.

In addition to the foregoing characters that are used in the diagnoses of species of *Colostethus*, other structural features and aspects of coloration differ interspecifically. Structural features include texture of the skin on the dorsum, which is smooth in most species, but with minute tubercles posterior to the sacral region in *C. aeruginosus*, *argyrogaster*, *craspedocephalus*, and *idiomelus*. The skin on the dorsum is finely shagreen in *C. mittermeieri*, *sordidatus*, and *sylvaticus*, and shagreen with minute tubercles posteriorly in *C. nexipus* and *C. poecilonotus*. The skin on the flanks usually has more texture (usually shagreen) than that on the dorsum; in most species, it is shagreen, but it is smooth in *C. aeruginosus*, *argyrogaster*, *elachyhistus*, and *utcubambensis*, and weakly granular in *C. craspedocephalus* and *C. sordidatus*. Distinct tubercles are present below the tympanum in *C. poecilonotus*. In most species of *Colostethus* in the Andes of northern Peru, the cloacal opening is directed posteriorly or posteroventrally at the upper level of the thighs; however, in *C. craspedocephalus* and *C. nexipus*, the cloacal sheath is relatively long and the opening is located at the midlevel of the thighs and directed ventrally.

None of the species of *Colostethus* in the Andes of northern Peru has supernumerary tubercles on the digits. Subarticular tubercles are always present and usually smaller on the toes than on the fingers; these tubercles are

small and round in most species, but they are distinctly subconical on the fingers of *C. elachyhistus*, *eleutherodactylus*, *insulatus*, *mittermeieri*, *ornatus*, and *sylvaticus*. Nuptial excrescences were not discernable on any males.

In addition to the combinations of longitudinal stripes and differences in ventral coloration, other features of the color pattern are noteworthy in some species. In most species of *Colostethus*, the dorsum of the head and body is dull brown with darker brown to black flecks, spots, or irregular marks, but a few species have distinctive colors—dull green in *C. aeruginosus*, reddish brown in *C. insulatus*, grayish brown in *C. leucophaeus*, grayish green with coppery brown markings in *C. pulcherrimus*, and olive brown to coppery brown in *C. sylvaticus*—or patterns—V-shaped marks in *C. idiomelus*, X-shaped mark connected to a teardrop-shaped mark posteriorly in *C. ornatus*, middorsal brown stripe in *C. spilotogaster*, and chevrons in some *C. sylvaticus*. The

dorsal surfaces of the hind limbs are tan or pale brown, usually with two to four dark brown transverse bars on each segment; there is only one bar on each segment in *C. ornatus*. Irregular dark brown markings are present on the dorsal surfaces of the hind limbs in *C. craspedocephus* and *C. spilotogaster*, and dark markings are absent on the dorsal surfaces in *C. argyrogaster*. A distinctive longitudinal dark brown stripe is present on the anterior surface of the thigh in *C. argyrogaster*, *craspedocephus*, and *poecilonotus*, and on the posterior surface in *C. argyrogaster*, *craspedocephus*, and *leucophaeus*. In contrast, *C. poecilonotus* has a pale cream stripe on the posterior surface; *C. insulatus*, on the anterior surface; *C. eleutherodactylus*, diagonal pale stripe on the anterior surface. Seven species (*C. elachyhistus*, *idiomelus*, *leucophaeus*, *ornatus*, *poecilonotus*, *sordidatus*, and *spilotogaster*) have longitudinal brown stripes on the upper arms; the mark is crescent-shaped in *C. sordidatus*.

IDENTIFICATION OF SPECIES

KEY TO THE SPECIES OF *COLOSTETHUS* IN NORTHERN PERU

- | | | | |
|---------------------------------------------------------------------------------------------------------------------------------|------------------------|-------------------------------------------------------------------------------------------------|-----------------------------|
| 1. Finger I < II; toes about one-half webbed; dorsolateral and oblique lateral stripes present..... | <i>C. nexipus</i> | 8. Oblique lateral stripe absent | <i>C. ornatus</i> |
| Finger I > II or I = II; webbing and stripes variable | 2 | Oblique lateral stripe present | 9 |
| 2. Finger I > II; digital discs expanded | 3 | 9. Dorsolateral stripe present..... | <i>C. utcuhambensis</i> |
| Fingers I and II equal in length; digital discs expanded or not | 11 | Dorsolateral stripe absent..... | 10 |
| 3. Lateral fringes present on fingers..... | 4 | 10. Oblique lateral stripe distinct, extending from orbit to groin | <i>C. argyrogaster</i> |
| Lateral fringes absent on fingers | 8 | Oblique lateral stripe diffuse, restricted to groin..... | <i>C. craspedocephus</i> |
| 4. Oblique lateral stripe present | 5 | 11. Dorsolateral stripe present | 12 |
| Oblique lateral stripe absent | 7 | Dorsolateral stripe absent..... | 15 |
| 5. Oblique lateral stripe present only in groin; toes about one-half webbed | <i>C. leucophaeus</i> | 12. Digital discs greatly expanded | 13 |
| Oblique lateral stripe extending from orbit to groin (may be indistinct anteriorly); toes with no more than basal webbing | 6 | Digital discs not or barely expanded | 14 |
| 6. Toes webbed basally; flanks gray with brown mottling; pair of dark spots laterally on throat | <i>C. insulatus</i> | 13. Oblique lateral stripe present | <i>C. eleutherodactylus</i> |
| Toes not webbed; flank black with pale flecks or streaks; throat cream with or without brown mottling | <i>C. pulcherrimus</i> | Oblique lateral stripe absent | <i>C. spilotogaster</i> |
| 7. Toes not webbed | <i>C. aeruginosus</i> | 14. Lateral fringes present on fingers..... | <i>C. sylvaticus</i> |
| Toes about one-fourth webbed | <i>C. mittermeieri</i> | Lateral fringes absent on fingers | <i>C. idiomelus</i> |
| | | 15. Oblique lateral stripe only on posterior part of body; toes about two-thirds webbed | <i>C. sordidatus</i> |
| | | Oblique lateral stripe extending from orbit to groin; toes no more than one-fourth webbed | 16 |
| | | 16. Lateral fringes present on fingers; toes at least webbed basally | <i>C. elachyhistus</i> |
| | | Lateral fringes absent on fingers; toes not webbed .. | <i>C. poecilonotus</i> |

CLAVE PARA LAS ESPECIES DE *COLOSTETHUS* DEL NORTE DEL PERU

1. Dedo manual I < Dedo manual II; dedos de los pies con membranas interdigitales que se extienden aproximadamente hasta la mitad de su longitud; líneas dorsolaterales y oblicuas presentes *C. nexipus*
Dedo manual I \geq Dedo manual II; membranas interdigitales y líneas en el dorso variables..... 2
2. Dedo manual I > II; discos de los dedos manuales expandidos 3
Dedo manual I con longitud similar a la del Dedo manual II; discos de los dedos manuales expandidos o no expandidos..... 11
3. Pliegues laterales presentes a lo largo de los dedos manuales..... 4
Dedos manuales sin pliegues laterales..... 8
4. Línea lateral oblicua presente 5
Línea lateral oblicua ausente 7
5. Línea lateral oblicua presente sólo en la ingle; dedos de los pies con membranas interdigitales que se extienden aproximadamente hasta la mitad de su longitud..... *C. leucophaeus*
Línea lateral se extiende desde la órbita ocular hasta la ingle (aunque puede ser indistinta anteriormente); dedos de los pies con membranas interdigitales solo en la base o sin membranas interdigitales 6
6. Dedos de los pies con membranas interdigitales basales; flancos del cuerpo color gris con un patrón irregular de manchas color café; garganta con un par de puntos oscuros (un punto en cada lado de la garganta).....*C. insulatus*
Dedos de los pies sin membranas interdigitales; flancos del cuerpo color negro con pequeñas manchas claras; garganta crema con o sin patrón irregular de manchas color café *C. pulcherrimus*
7. Dedos de los pies sin membranas interdigitales....*C. aeruginosus*
8. Línea lateral oblicua ausente *C. ornatus*
Línea lateral oblicua presente 9
9. Línea dorsolateral presente.....*C. utubambensis*
Línea dorsolateral ausente 10
10. Línea lateral oblicua evidente y que se extiende desde la órbita ocular hasta la ingle..... *C. argyrogastrer*
Línea lateral oblicua difusa y restringida a la ingle *C. craspediceps*
11. Línea dorsolateral presente..... 12
Línea dorsolateral ausente 15
12. Discos de los dedos manuales muy expandidos .. 13
Discos de los dedos manuales no expandidos o apenas expandidos 14
13. Línea lateral oblicua present *C. eleutherodactylus*
Línea lateral oblicua ausente *C. spilotogaster*
14. Pliegues laterales presentes a lo largo de los dedos manuales..... *C. sylvaticus*
Dedos manuales sin pliegues laterales... *C. idiomelus*
15. Línea lateral oblicua evidente únicamente en la parte posterior del cuerpo; dedos de los pies con membranas interdigitales que se extienden hasta aproximadamente 2/3 de su longitud *C. sordidatus*
Línea lateral oblicua se extiende desde la órbita ocular hasta la ingle; dedos de los pies con membranas interdigitales que no se extienden más allá de 1/4 de su longitud..... 16
16. Dedos manuales con pliegues laterales; dedos de los pies con membranas interdigitales presentes por lo menos basalmente *C. elachyistus*
Dedos manuales sin pliegues laterales; dedos de los pies sin membranas interdigitales *C. poecilonotus*

ACCOUNTS OF THE SPECIES

Colostethus aeruginosus new species

Holotype.—KU 211940, an adult female from the east slope of Abra Pardo de Miguel (05°46' S, 77°42' W), 2180 m, Provincia de Rioja, Departamento de San Martín, Peru; one of a series collected by Fernando Cuadros, Michael E. Morrison, and John J. Wiens on 31 January and 01 February 1989.

Paratypes.—KU 211941–43 and MHNSM 6225–27 with same data as holotype; KU 211945 from the east slope of Abra Pardo de Miguel, 1980 m, Provincia de Rioja, Departamento, San Martín, Peru.

Diagnosis.—A moderately large species of *Colostethus* with the following characteristics: (1) maximum SVL of males 25.0 mm, of females 29.2 mm; (2) disc on Finger III

(7) outer tarsal fold and tarsal tubercle absent; inner tarsal fold curved, distinct on distal half of tarsus; (8) webbing absent between toes; (9) dorsolateral stripe absent; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) gular-chest region brown with cream spots; (13) posterior part of abdomen mottled or cream; (14) sexual dimorphism in ventral coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

The only other species in Ecuador and Peru that has Finger I longer than Finger II and lacks longitudinal stripes is *Colostethus mittermeieri*; this species differs from *C. aeruginosus* by having the toes about one-fourth webbed and having a cream venter with a pair of brown spots on the throat.

Description.—(N = 8: 5 males, 1 female, 2 juveniles). Body moderately robust; head slightly wider than long; head length 32.4–37.1% (\bar{x} = 35.6%) of SVL; head width 36.3–39.0% (\bar{x} = 37.7%) of SVL; snout moderately long, bluntly rounded in dorsal and lateral profiles; loreal region slightly concave; nostrils barely protuberant, anterior border at level slightly posterior to anterior margin of lower jaw; eye–nostril distance 72.4–78.6% (\bar{x} = 74.5%) of length of eye; supratympanic bulge weak¹, covering upper edge of tympanum; tympanic annulus distinctly elevated; length of tympanum 51.7–62.9% (\bar{x} = 58.9%) length of eye, separated from eye by distance about one-fifth length of eye.

Forelimb moderately long, slender; Finger I noticeably longer than Finger II; fingers unwebbed, bearing broad lateral fringes; Finger III not swollen in males; terminal discs expanded, width about half again width of penultimate phalanges; subarticular tubercles rounded; supernumerary tubercles absent; palmar tubercle large, round; thenar tubercle small, elliptical; nuptial excrescences absent. Hind limb short, robust; tibia length 42.8–44.7% (\bar{x} = 44.0%) SVL; foot length 41.1–42.6% (\bar{x} = 41.9%) SVL; outer tarsal fold and tarsal tubercle absent; inner tarsal fold flaplike, forming shallow sigmoid on distal half of tarsus; inner metatarsal tubercle small, elliptical; outer metatarsal tubercle small, subconical; toes unwebbed, bearing broad lateral fringes; terminal discs expanded, width about half again width of penultimate phalanges; subarticular tubercles small, rounded; supernumerary tubercles absent.

Skin on dorsum of head, body, and hind limbs smooth with scattered tubercles posteriorly on dorsum and on hind limbs; skin on flanks and ventral surfaces smooth; cloacal opening directed posteroventrally at midlevel of thighs; cloacal sheath short. Tongue long, widest and shallowly

notched posteriorly, free behind for about one-third of its length; median lingual process absent.

Color in preservative: Pale longitudinal stripes absent. In females, dorsum of head and body black with faint tan flecks on head; flanks black with cream spots; upper lip cream with faint gray markings; dorsal surfaces of limbs black with indistinct tan spots; anterior and posterior surfaces of thighs brownish black with irregular, small cream spots; throat, chest, anterior two-thirds of belly, and ventral surfaces of limbs black with cream spots (Fig. 3); posterior one-third of belly and proximal surfaces of thighs cream; palmar and plantar surfaces dark gray. In males, dorsum dull brown with faint irregular darker brown markings; limbs tan with dark brown transverse bars; throat and chest dark brown with cream spots; belly and ventral surface of limbs cream.

Color in life Female holotype.—Dorsum dull green with faint bluish tint; bluish cream flecks on flanks; dorsal surfaces of digital scutes white, contrasting with bordering gray surfaces; throat chest, and anterior part of belly olive brown with cream spots; posterior part of belly and ventral surfaces of thighs dark yellow; iris brown with cream ring around pupil (Fig. 5A).

Measurements of holotype (in mm): SVL 29.2, tibia length 14.0, foot length 13.5, head width 10.4, head length 9.5, eye–nostril distance 2.6, length of eye 3.5, length of tympanum 2.1.

Distribution and ecology.—This species is known from two localities at elevations of 1980 and 2180 m along the road from Abra Pardo de Miguel to Moyobamba on the steep east slope of the northern part of the Cordillera Central in northern Peru (Fig. 4). The frogs were associated with small streams in cloud forest; all were under rocks at the edges of streams by day.

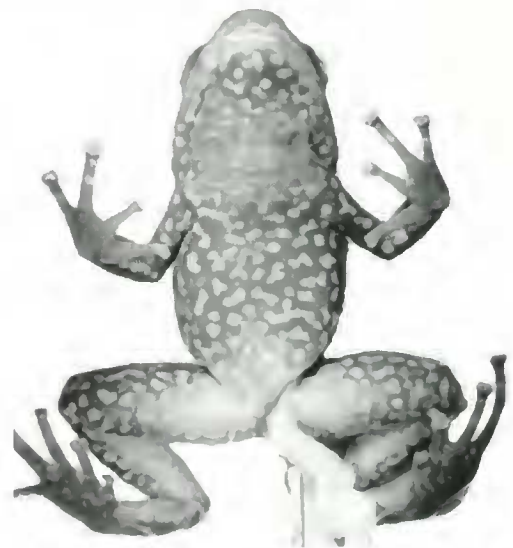


Fig. 3. *Colostethus aeruginosus*, KU 211940, female venter, 29.2 mm SVL

¹ I use the term "bulge" instead of "fold." According to Grant (2004), the bulge is formed by a slip of the *m. depressor mandibulae* and is not a dermal modification as is the fold of skin usually referred to as a supratympanic fold.

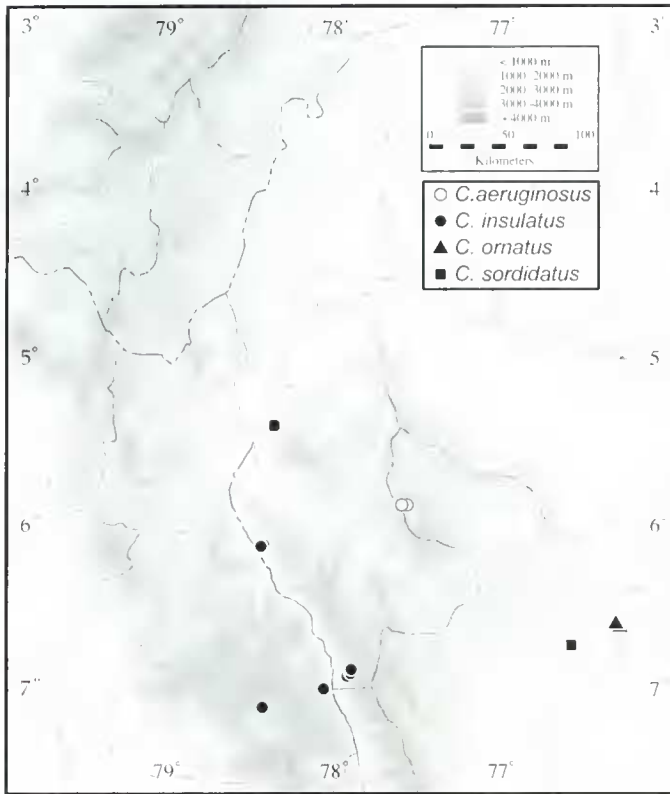


Fig. 4 Localities of occurrence of four species of *Colostethus*.

Etymology.—The specific name is Latin meaning full of verdigris and refers to the dull bluish green dorsal coloration.

Remarks.—At least some of the apparent sexual differences in coloration may be related to size. Three juveniles (KU 211945, MHNSM 6227) with SVLs of 20.5 and 18.8 mm have uniformly cream venters and bars on the limbs that are more distinct than those in males having SVLs of 22.1–25.0 mm.

Colostethus argyrogastrus Morales and Schulte

Colostethus argyrogastrus Morales and Schulte, 1993:98. Holotype: MHNSM 14256 from Imazá, Provincia Bagua Grande, Departamento de Amazonas, Peru.

Diagnosis.—A small species of *Colostethus* with the following characteristics: (1) SVL in males 17.5–19.8 mm, in females 19.0–22.1 mm; (2) disc on Finger III expanded; (3) Finger I longer than Finger II; (4) lateral fringes absent on fingers; (5) disc on Toe IV expanded; (6) lateral fringes absent on toes; (7) outer tarsal fold absent; (8) webbing basal between Toes III and IV, absent between other toes; (9) dorsolateral stripe absent; (10) oblique lateral stripe present; (11) ventrolateral stripe present; (12) gular-chest region uniform cream; (13) abdomen bright silver; (14) males with orange inguinal region in life; (15) median

lingual process absent; (16) Finger III not swollen in males; (17) testes white.

Few species of *Colostethus* in Ecuador and Peru lack lateral fringes on the digits and have Finger I longer than Finger II. Of these, only *C. argyrogastrus* and *C. ornatus* have ventrolateral stripes; the latter differs from *C. argyrogastrus* by having dorsolateral stripes and by having a lemon yellow belly instead of a silver-colored venter; likewise, *C. utubambensis* has dorsolateral stripes. *Colostethus mittemeieri* differs by lacking all longitudinal stripes, and *C. craspedocephalus* differs by having no webbing between the toes and a diffuse (instead of distinct) oblique lateral stripe.

Description.—($N = 5$: 2 males, 3 females) Body moderately slender; head longer than wide; head length 33.9–38.5% ($\bar{x} = 36.6$) of SVL; head width 29.0–32.3% ($\bar{x} = 31.1$) of SVL; snout long, bluntly rounded in dorsal view, acutely rounded in profile; loreal region flat; nostrils not protuberant, anterior edge slightly posterior to anterior end of lower jaw; eye–nostril distance 63.3–75.9% ($\bar{x} = 69.3\%$) of SVL; eye; supratympanic bulge diffuse, obscuring posterodorsal part of tympanum; length of tympanum 44.8–59.1% ($\bar{x} = 50.1$) of SVL; length of eye, separated from eye by distance about one-tenth length of eye.

Forelimb long, slender; Finger I longer than Finger II; fingers unwebbed, lacking lateral fringes; Finger III not swollen in males (Morales and Schulte, 1994); terminal discs expanded, about half again width of penultimate phalanges; subarticular tubercles rounded; supernumerary tubercles absent; palmar tubercle moderately small, round, partially bifid; thenar tubercle large, elliptical; presence of nuptial excrescences absent. Hind limb moderately short, robust; tibia length 41.6–46.0% ($\bar{x} = 44.4\%$) of SVL; foot length 40.3–42.1% ($\bar{x} = 41.2\%$) of SVL; outer tarsal fold absent; inner tarsal fold barely discernible, continuous with small tarsal tubercle on distal one-third of tarsus; inner metatarsal tubercle small, ovoid; outer metatarsal tubercle small, subconical; toes unwebbed, lacking lateral fringes; terminal discs slightly expanded, about half again width of digits; subarticular tubercles small, rounded; supernumerary tubercles absent.

Skin on all surfaces smooth, with a few low, scattered tubercles posteriorly on dorsum of body; cloacal opening directed posteroventrally at upper level of thighs; cloacal sheath short. Tongue cordiform, shallowly notched posteriorly, free behind for about one-half its length; median lingual process absent.

Color in preservative: Dorsum of head and body brown without darker markings; flanks uniform dark brown, color continuing anteriorly as brown stripe through upper two thirds of tympanum, loreal region, and around tip of snout; dorsolateral stripe absent; oblique lateral stripe pale tan, extending from posterior corner of orbit to groin; creamy white labial stripe through lower one third



A. *Colostethus aeruginosus*, KU 211940, female, 29.2 mm SVL.



B. *Colostethus craspediceps*, KU 211952, female, 19.5 mm SVL.



C. *Colostethus elachyistius*, KU 212520, female, 21.3 mm SVL.



D. *Colostethus insulatus*, KU 211833, female, 22.5 mm SVL.



E. *Colostethus eleutherodactylus*, KU 211814, female, 22.7 mm SVL.



F. *Colostethus idiomelus*, KU 211887, female, 24.9 mm SVL.



G. *Colostethus idiomelus*, KU 211884, female, 23.0 mm SVL.



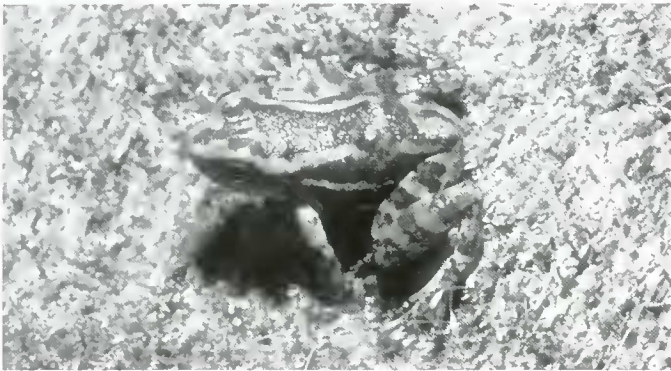
H. *Colostethus idiomelus*, KU 211884, female, 23.0 mm SVL.



A. *Colostethus insulatus*, KU 211857, female, 22.0 mm SVL.



B. *Colostethus leucophaeus*, KU 211879, female, 26.1 mm SVL.



C. *Colostethus nexipus*, KU 211805, female, 22.8 mm SVL.



D. *Colostethus ornatus*, KU 211951, female, 17.3 mm SVL.



E. *Colostethus pulcherrimus*, KU 211946, female, 28.0 mm SVL.



F. *Colostethus sylvaticus*, KU 181667, female, 28.7 mm SVL.



G. *Colostethus sordidatus*, KU 211860, female, 33.0 mm SVL.



H. *Colostethus sordidatus*, KU 211861, female, 36.1 mm SVL.

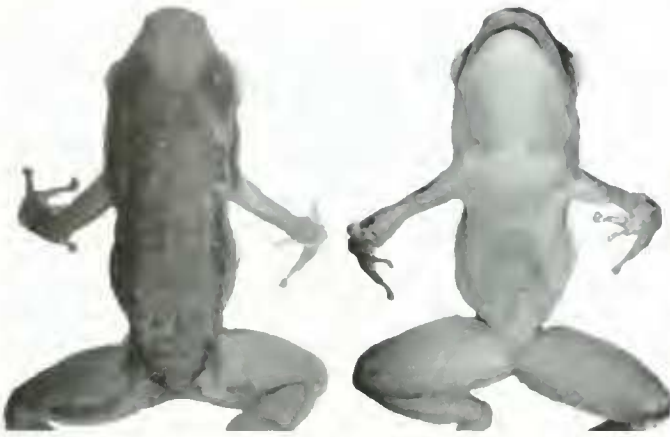


Fig. 7. *Colostethus argyrogastrer*, MHNSM 14257, female, 22.1 mm SVL.

of tympanum and continuous with ventrolateral stripe extending to groin; forelimbs tan; dorsal surfaces of hind limbs tan; anterior surfaces of thighs tan with dark brown longitudinal stripe; posterior surfaces of thighs brown with longitudinal dark brown stripe. Venter uniform creamy white; palmar surfaces tan; plantar surfaces brown (Fig. 8).

Color in life: "Dorsum pale brown with granules on posterior part of body dark brown; flanks dark brown; oblique lateral line brilliant silver; dorsal surfaces of thighs cream; posterior surfaces of thighs and inner surfaces of shanks orange; inguinal region diffuse orange; white mark on either side of cloaca extending onto posterior surface of thigh; throat and chest cream; abdomen bright silver; iris bronze" (translation from Spanish in Morales and Schulte, 1994:100). Sexual dimorphism in coloration is the orange inguinal region in living males.

Distribution and ecology.—This small species is known from two localities in the Río Cainarachi drainage east of the Cordillera Central and from two localities in the middle Río Marañón near the northern end of the Cordillera Central (Fig. 8). These localities are at elevations of 500–650 m in partially cutover lowland humid tropical forest and dry forest.

Remarks.—The foregoing description is based on three paratypes (MHNSM 1808–09 and 14257) and two additional specimens (KU 196717 and LSUMNS 32523).

Colostethus craspedocephus new species

Holotype.—KU 211952, an adult female, from 30 km southwest of Zapatero (about 10 km NE San José de Sisa [ca. 06°45' S, 76°33' W], 500 m, Provincia de Lamas, Departamento de San Martín, Peru; one of a series collected by William E. Duellman and Rainer Schulte on 13 February 1989.

Paratypes.—KU 211953–59 collected with the holotype.

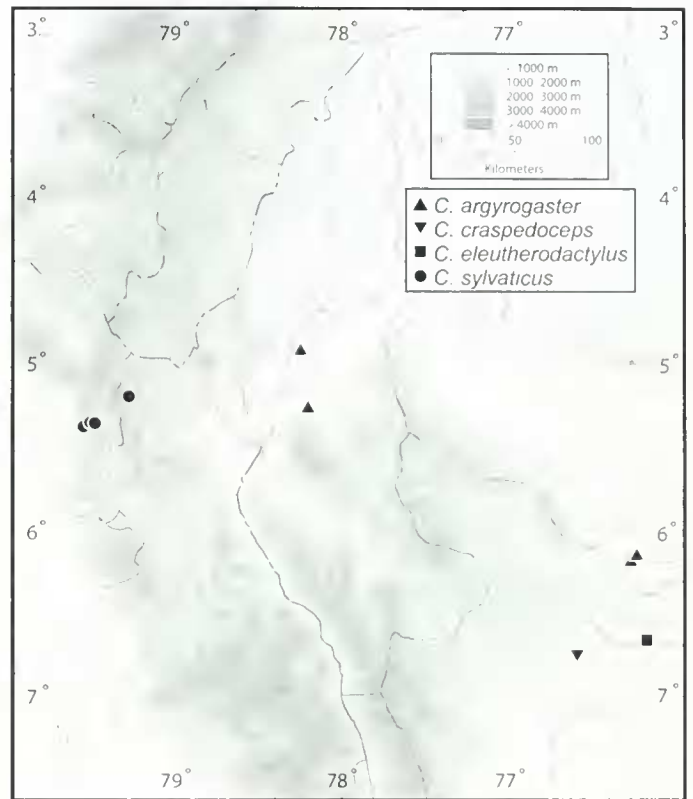


Fig. 8. Localities of occurrence of four species of *Colostethus*.

Diagnosis.—A small species of *Colostethus* with the following characteristics: (1) maximum SVL of males 19.1 mm, of females 20.5 mm; (2) disc on Finger III expanded, about half again width of penultimate phalange; (3) Finger I longer than Finger II, (4) lateral fringes absent on fingers; (5) disc on Toe IV expanded, about twice width of penultimate phalange; (6) lateral fringes absent on toes; (7) outer and inner tarsal folds absent; low, indistinct outer tarsal tubercle present; (8) webbing absent between toes; (9) dorsolateral stripe present; (10) oblique lateral stripe diffuse, present in groin only; (11) ventrolateral stripe absent; (12) gular-chest region cream; (13) abdomen cream; (14) sexual dimorphism in ventral coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

Twelve other species in Ecuador, Peru, and Amazonian Brazil resemble *Colostethus craspedocephus* in having Finger I longer than Finger II and in having dorsolateral stripes, but no oblique lateral stripe.² One of these, *C. talamancae*, is slightly larger (maximum SVL 24 mm), has moderate webbing between the toes and a ventrolateral stripe, and is restricted to the Chocóan Region. The other 11 species are

²Most specimens of *Colostethus trilineatus* have a pale streak anterior to the groin (Grant and Rodríguez, 2001); *C. marchesianus* has a diffuse pale line or series of diffuse pale spots in the groin or extending anteriorly to midflank or near to the insertion of the arm (Caldwell et al., 2002).

Amazonian and belong to the *Colostethus trilineatus* Group as defined by Morales (2002). All of these have ventrolateral stripes; seven of the species (*C. fuscellus*, *gasconi*, *marchesianus*, *ornatus*, *sumptuosus*, *trilineatus*, *vanzolinius*) also differ from *C. craspedocephus* by having Finger III swollen in males. Six species (*C. conspicuus*, *gasconi*, *marchesianus*, *masniger*, *sumptuosus*, *vanzolinius*) also differ by having lateral fringes on the toes (also on fingers in *C. vanzolinius*). Five species (*C. insperatus*, *ornatus*, *sumptuosus*, *trilineatus*, *vanzolinius*) are distinguished by having webbing between Toes III and IV.

Description.—($N = 8$: 1 male, 5 females, 2 juveniles). Body robust; head slightly longer than wide; head length 35.6–38.5% ($\bar{x} = 37.8\%$) of SVL; head width 33.2–35.9% ($\bar{x} = 34.4\%$) of SVL; snout moderately long, bluntly rounded in dorsal view, rounded above and inclined posteroventrally in profile; loreal region flat; nostrils noticeably protuberant laterally, anterior margins at level of anterior margin of lower jaw; eye-nostril distance 68.0–76.9% ($\bar{x} = 72.2\%$) eye; supratympanic bulge diffuse, covering posterodorsal edge of tympanum; otherwise, tympanic annulus distinct; length of tympanum 48.0–63.0% ($\bar{x} = 55.3\%$) length of eye, separated from eye by distance about one-eighth length of eye.

Forelimb short, moderately robust; Finger I distinctly longer than Finger II; fingers not webbed, lacking lateral fringes; Finger III not swollen in male; terminal discs expanded, about half again width of penultimate phalanges; subarticular tubercles rounded; supernumerary tubercles absent; palmar tubercle large, round; thenar tubercle small, elliptical; nuptial excrescences absent. Hind limb short, robust; tibia length 43.5–45.3% ($\bar{x} = 44.5\%$) SVL; foot length 41.4–42.9% ($\bar{x} = 42.2\%$) SVL; tarsal folds absent; outer tarsal tubercle low, indistinct; inner metatarsal tubercle elliptical; outer metatarsal tubercle rounded; toes unwebbed; lateral fringes absent on toes; terminal discs expanded, about twice width of penultimate phalanges; subarticular tubercles small, subconical; supernumerary tubercles absent.

Skin on dorsum of body and hind limbs, and venter smooth; skin on flanks weakly granular; cloacal opening directed ventrally at midlevel of thighs; cloacal sheath long. Tongue long, widest and shallowly notched posteriorly, free behind for about one-half of its length; median lingual process absent; vomerine odontophores absent.

Color in preservative: Dorsum of head and body brown with or without darker brown dashes middorsally; flanks brown; dorsolateral stripe pale tan; stripe narrow and distinct across tip of snout, along canthus rostralis and outer edge of eyelid, becoming wider and somewhat diffuse on body and continuous to supracloacal region, bordered below for its entire length by wider dark brown stripe; oblique lateral stripe short, diffuse, restricted to groin; ventrolateral stripes absent; upper lip creamy tan. Forelimbs tan with irregular brown marks on forearm and longitudinal brown stripe on anterior edge of upper arm;

dorsal surfaces of hind limbs pale brown with irregular darker brown markings; anterior and posterior surfaces of thighs pale brown with diffuse darker brown longitudinal stripes, fragmented on posterior surfaces of thighs in some individuals. Venter cream, with male having grayish-brown throat and chest; palmar and plantar surfaces brown.

Coloration in life: Dorsum brown with yellowish-tan dorsolateral stripes, distinct on head, diffuse on body, bordered below by dark brown; side of head below brown stripe and dorsal surfaces of upper arms dull yellow; dorsal surfaces of digital scutes gray; flanks creamy tan with irregular brown spots (Fig. 5B); belly creamy yellow with greenish tint; ventral surfaces of limbs dull yellow; throat and chest of male brown; iris coppery bronze with median horizontal dark brown streak.

Measurements of holotype (in mm): SVL 19.5, tibia length 8.8, foot length 8.3, head width 7.0, head length 7.7, eye-nostril distance 2.0, length of eye 2.7, length of tympanum 1.9.

Tadpoles.—Tadpoles associated with this species are from the type locality and include seven back-riding tadpoles and eight free-swimming tadpoles from a pool in a stream in a rocky ravine. One male with a SVL of 19.1 mm was transporting seven tadpoles on its back. Back-riding tadpoles have body lengths of 3.7–4.8 mm ($\bar{x} = 4.36$) and total lengths of 11.0–12.9 mm ($\bar{x} = 11.91$). These tadpoles have jaw sheaths and a LTRF of 2(1)/2. In life, the tadpoles were dark brown. In preservative, the body is dark brown dorsally, becoming cream ventrally; the caudal musculature is cream with brown reticulations, and scattered guanophores are present on the body, caudal musculature, and translucent caudal fins. Five of the free-swimming tadpoles are in Stage 25 and have body lengths of 6.5–9.8 mm ($\bar{x} = 8.72$) and total lengths of 15.9–23.7 mm ($\bar{x} = 20.68$). Three tadpoles in Stages 31, 34, and 35, have body lengths of 10.0, 10.0, 11.5 mm, and total lengths of 24.5, 25.3, and 27.0 mm, respectively.

A typical tadpole (KU 215610) in Stage 34 has a body length of 10.0 mm and a total length of 25.3 mm; body ovoid, wider (5.5 mm) than high (4.5 mm); snout rounded in dorsal view and in profile; nares directed dorsolaterally at point midway between tip of snout and orbits; eyes moderately large (1.2 mm), situated dorsally, directed dorsolaterally, not visible from below; interorbital distance 2.1 mm; spiracle sinistral; tube short, attached to body throughout its length; spiracular opening directed posteriorly just below midline at about midlength of body; cloacal tube dextral, short, cone-shaped, attached to ventral fin. Caudal musculature robust, equal height throughout proximal third of tail, gradually diminishing to pointed tip; dorsal fin originating on caudal musculature, highest at about two-thirds length of tail, gradually diminishing

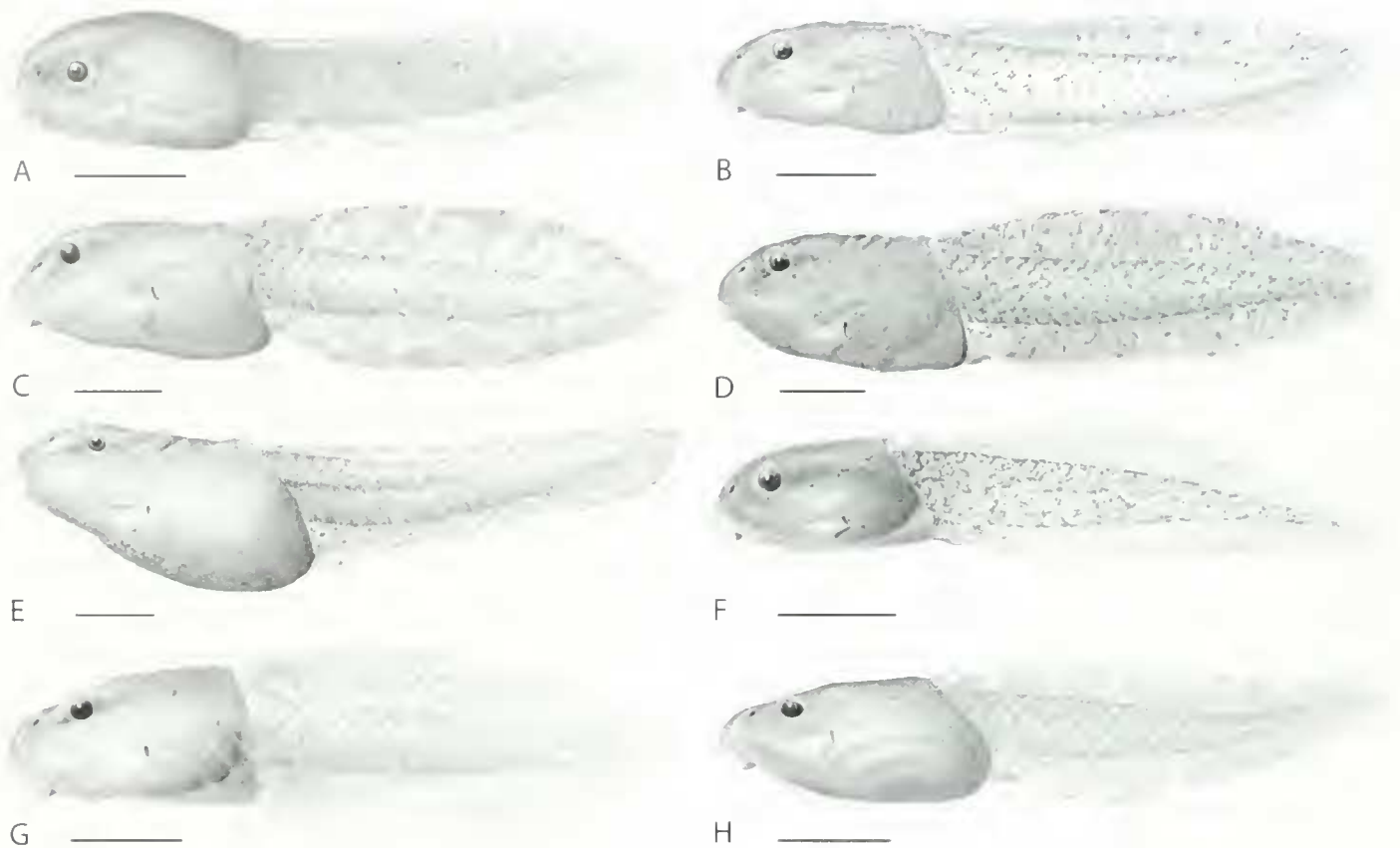


Fig. 9. Tadpoles of eight species of *Colostethus* from the Andes of northern Peru. A. *C. craspedocephus*, KU 215610, Stage 34, 25.3 mm total length. B. *C. clachylustus*, KU 219754, Stage 34, 32.5 mm total length. C. *C. idiomelas*, KU 215607, Stage 34, 34.7 mm total length. D. *C. insulatus*, KU 215600, Stage 34, 38.3 mm total length. E. *C. leucophaeus*, KU 215603, St. 28, 42.5 mm total length. F. *C. nexipus*, KU 215594, Stage 37, 30.5 mm total length. G. *C. sordidatus*, KU 215611, Stage 25, 30 mm total length. H. *C. sylvaticus*, KU 181869, Stage 33, 29.4 mm total length. Scale bars = 5 mm.

to acutely rounded tip; ventral fin originating on body, highest at about three-fifths length of tail; at midlength of tail; heights of dorsal and ventral fins about equal, less than height of caudal musculature (Fig. 9A).

Width of oral disc 2.8 mm, directed anteroventrally; median half of anterior labium bare; elsewhere, labia bearing single row of moderately long, pointed marginal papillae; labia having shallow lateral folds; submarginal papillae absent. Jaw sheaths slender, finely serrate; anterior sheath in form of broad arch; posterior sheath broadly V-shaped; LIRI: 2(1)/3; A_2 slightly longer than others.

In life, body and tail gray. In preservative, dorsum and sides of body brown; belly cream; caudal musculature pale creamy tan with small, irregular brown spots; caudal musculature translucent with brown spots; guanophores scattered on body and tail (Fig. 9A).

Distribution and ecology.—This species is known only from the type locality at the eastern base of the northern part of Cordillera Central (Fig. 8); this is a stream in a shallow ravine in cutover humid tropical forest. The frogs were active on wet boulders in the stream by day. Tadpoles of

Colostethus sordidatus were found in the same stream as tadpoles of *C. craspedocephus*.

Etymology.—The specific name is an adjective derived from the Greek *kraspedon* meaning edge or border and the Greek *kephale* meaning head. The name refers to the pale stripe bordering the anterior and lateral margins of the head.

Colostethus clachylustus Edwards

Colostethus clachylustus Edwards, 1971:149. Holotype: KU 120540 from Loja, 2150 m, Provincia de Loja, Ecuador.

Diagnosis.—A moderately small species of *Colostethus* with the following characteristics: (1) maximum SVL of males 24.1 mm, of females 24.8 mm; (2) disc on Finger III not, or only slightly, expanded; (3) Fingers I and II equal in length; (4) lateral fringes present on fingers; (5) disc on Toe IV slightly expanded; (6) lateral fringes present on toes; (7) outer tarsal fold weak or absent; inner tarsal fold curved on distal third of tarsus; (8) toes about one-third webbed; (9) dorsolateral stripe absent; (10) oblique lateral stripe present; (11) ventrolateral stripe absent; (12) gular-chest region with pair of dark marks; (13) abdomen with white spots;

(14) no conspicuous sexual dimorphism in coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

Colostethus elachylistus resembles *C. awa*, *infraguttatus*, and *vertebralis* in having an oblique lateral stripe and pair of dark marks on the gular-chest region. It differs from *C. vertebralis* in ventral coloration and by lacking a middorsal stripe, from *C. awa* by having a well-defined, continuous oblique lateral stripe (diffuse and fragmented in *C. awa*), and from *C. infraguttatus* by having more extensive webbing (toes webbed basally in *C. infraguttatus*). *Colostethus eleutherodactylus*, *C. sordidatus*, and *C. sylvaticus* also have Fingers I and II equal in length, but these species lack webbing between the toes, and *C. eleutherodactylus* and *C. sylvaticus* have dorsolateral stripes.

Description.—($N = 36$: 20 males, 16 females). Body moderately robust; SVL in males 16.7–19.8 ($\bar{x} = 18.4$) mm, in females 18.6–23.4 ($\bar{x} = 20.4$) mm; head slightly longer than wide; head length 32.6–40.1% ($\bar{x} = 36.4\%$) of SVL; head width 30.9–37.6% ($\bar{x} = 34.6\%$) of SVL; snout short, bluntly rounded in dorsal view, rounded in lateral profile; loreal region flat; nostrils slightly protuberant laterally, anterior border; eye–nostril distance 50.0–68.0% ($\bar{x} = 57.7\%$) eye length; supratympanic bulge low, diffuse, covering posterodorsal part of tympanum; length of tympanum 48.3–62.1% ($\bar{x} = 54.5\%$) length of eye, separated from eye by distance about one-tenth length of eye.

Forelimb moderately short, slender; Fingers I and II equal in length; fingers unwebbed, bearing narrow lateral fringes; Finger III not swollen in males; terminal discs not or slightly expanded; subarticular tubercles subconical; supernumerary tubercles absent; palmar tubercle large, round; thenar tubercle elliptical; nuptial excrescences absent. Hind limb short, robust; foot longer than tibia; tibia length 42.9–50.6% ($\bar{x} = 47.1\%$) SVL; foot length 44.4–52.2% ($\bar{x} = 48.9\%$) SVL; outer tarsal fold weak or absent; inner tarsal fold conspicuous, curved on distal third of tarsus; inner metatarsal tubercle ovoid; outer metatarsal tubercle subconical; toes at least partially webbed, usually about one-third webbed; webbing formula $I(1^+-2^-)-(2^-2^+)II(2^-2^+)-(3^-3^+)III(2^+-3^+)-(3^+-4^-)IV(3^+-4^-)-(2^+-3^+)V$; toes with narrow lateral fringes; terminal discs slightly expanded, no more than half again width of penultimate phalanges; subarticular tubercles small, round; supernumerary tubercles absent.

Skin on all surfaces smooth; small, scattered tubercles present postsacrally in some specimens; cloacal opening directed posteriorly at upper level of thighs; cloacal sheath short. Tongue half again as long as wide, widest and distinctly notched posteriorly, free behind for about two-thirds of its length; median lingual process absent.

Color in preservative: Dorsum of head and body brown with darker brown irregular spots; flanks brown

with small white spots ventrally in some specimens; dark brown stripe continuous from nostrils, below canthus, along supratympanic area to flanks; dorsolateral stripe absent; oblique lateral stripe creamy tan, extending from groin to edge of upper eyelid or just posterior to eye, continuous with irregular edges on anterior surface of thigh; ventrolateral stripe absent (except in one female). Upper arm creamy tan with brown stripe on anterior surface; forearm creamy tan with or without irregular brown cross bars; dorsal surfaces of hind limbs tan with two or three dark brown transverse bars extending onto posterior surfaces of thighs; upper lip dull tan. Venter tan with or without pair of brown spots posterolaterally on throat; some females with gray mottling enclosing dull white spots on abdomen; one female with small brown spots on throat and abdomen; palmar and plantar surfaces tan.

Color in life: Dorsum variable from pale olive to brown; oblique lateral stripe pale yellow to tan, usually narrowly bordered by dark brown or black (Fig. 5C). Specimens from Huancabamba.—Dorsum brown with dark brown or black markings; flanks dull brown; oblique lateral stripe dull creamy tan; abdomen creamy yellow with gray mottling; throat creamy white with gray suffusion; iris grayish brown. Specimens from Canchaque.—Dorsum yellowish olive with black markings; oblique lateral stripe silvery white; venter white; iris reddish brown.

Tadpoles.—Six adults were transporting tadpoles in February and March. A female (KU 212514) having a SVL of 24.5 mm was carrying five tadpoles (KU 212488) at Ayabaca, Departamento de Piura, Peru, on 21 February 1989; other adults transporting tadpoles are males from Abra de Porculla, Departamento de Piura, and 1 km S Cajabamba, Departamento de Cajamarca. Size and development of keratinized structures in the oral disc vary (Table 3); the smallest individuals lack differentiated intestines, and the body cavity is filled with yolk.

Table 3. Measurements (in mm) and labial tooth row formula (LTRF) of transporting adults and back-riding tadpoles of *Colostethus elachylistus*. Range of variation followed on next line by mean.

Adult SVL	Sex	N	Body length	Total length	LTRF
24.5	Male	5	3.7–3.8 3.75	10.4–10.6 10.53	2 1–2 2
21.8	Female	12	3.4–3.7 3.58	10.0–10.4 10.14	1 0–1 1
18.7	Female	11	3.3–3.5 3.38	9.8–10.1 9.97	0/0–1 0
18.3	Female	7	6.5–7.4 6.90	15.4–17.4 16.68	2/2
18.3	Female	6	3.6–3.7 3.68	9.9–10.3 10.1	1 1
17.8	Female	14	3.3–3.5 3.40	10.2–10.4 10.26	1/0–1/2

Table 4. Measurements (in mm) of free-swimming tadpoles of *Colostethus elachyistus* from the vicinity of Canchaque, Departamento de Piura, Peru. Range of variation followed by mean in parentheses.

Stage	N	Body length	Total length
25	2	7.8–9.0 (\bar{x} = 8.4)	20.2–22.4 (\bar{x} = 21.20)
26	5	5.1–7.0 (\bar{x} = 6.26)	15.0–18.5 (\bar{x} = 16.62)
27	7	7.4–8.5 (\bar{x} = 7.98)	19.2–27.2 (\bar{x} = 22.29)
28	3	8.1–8.9 (\bar{x} = 8.63)	22.1–26.3 (\bar{x} = 24.43)
29	1	9.3	22.6
30	2	8.9	20.6–25.9 (\bar{x} = 23.25)
32	1	9.6	29.0
33	3	10.3–13.3 (\bar{x} = 11.30)	30.5–38.2 (\bar{x} = 33.41)
34	5	10.1–12.2 (\bar{x} = 11.28)	31.3–33.8 (\bar{x} = 33.74)
35	4	10.9–12.3 (\bar{x} = 11.53)	32.7–36.6 (\bar{x} = 34.58)
36	3	10.6–12.5 (\bar{x} = 11.27)	31.8–38.2 (\bar{x} = 35.87)
39	2	10.5–11.7 (\bar{x} = 11.10)	36.2–36.5 (\bar{x} = 36.35)
40	1	12.6	38.2
43	1	11.6	35.1

Free-swimming tadpoles have been found in pools in streams in January–March. Series of tadpoles from the vicinity of Canchaque, Departamento de Piura, are in Stages 25–43 (Table 4). A typical tadpole in Stage 34 (KU 219754) has a body length of 10.8 mm and a total length of 32.5 mm; body ovoid, much wider (7.2 mm) than high (4.7 mm); snout bluntly rounded in dorsal view and in profile; nares directed anterolaterally at point about midway between tip of snout and orbits; eyes large (1.5 mm), situated dorsally, directed dorsolaterally, not visible from below; interorbital distance 1.9 mm; spiracle sinistral; tube short, attached to body throughout its length; spiracular opening directed posterodorsally well below midline at about midlength of body; cloacal tube dextral, short, attached to ventral fin. Caudal musculature robust, equal height throughout proximal third of tail, gradually diminishing to pointed tip; dorsal fin originating on caudal musculature, highest at about three-fourths length of tail, gradually diminishing to acutely rounded tip; ventral fin originating on body, highest at about two thirds length of tail; at midlength of tail, height of dorsal fin greater than that of ventral fin, much less than height of caudal musculature (Fig. 9B).

Width of oral disc 3.0 mm, directed anteroventrally; median half of anterior labium bare; elsewhere labia bear single row of moderately long, pointed marginal papillae; labia having shallow lateral folds; submarginal papillae absent. Jaw sheaths moderately robust, coarsely serrate; anterior sheath in form of broad arch; posterior sheath broadly V-shaped; LTRF 2(1)/3; A_1 slightly longer than others.

In life, body olive-gray; tail yellow proximally, becoming more orange distally, flecked with gray. In preservative, dorsum and sides of body brown; belly translucent gray;

caudal musculature pale creamy tan with brown flecks; caudal musculature translucent with brown flecks (Fig. 9B).

Distribution and ecology.—As presently recognized, this species has the largest geographic and elevational distribution of all *Colostethus* in northern Peru (Fig. 10). It ranges from the vicinity of San Lucas, Ecuador, to Cajabamba, Peru, an airline distance of about 425 km. The elevational range in northern Peru is 710–2760 m; the species occurs in thorn forest, dry forest, montane dry forest, and humid montane forest. On the western slopes of the Cordillera de Huancabamba, it occurs sympatrically with *C. sylvaticus* at elevations of 1920–2590 m. At Cutervo, Departamento de Cajamarca, it occurs sympatrically with *C. pulcherrimus*.

In cultivated areas, such as the vicinity of Huancabamba, Peru, and Macará Ecuador, the frogs inhabit irrigation ditches. At other places in thorn forest or dry forest, the frogs seem to be restricted to the immediate vicinity of small streams, a habitat in which they also are abundant in humid montane forest.

Remarks.—The foregoing description is based on specimens from the vicinities of Huancabamba and Canchaque, Departamento de Piura, Peru. Duellman and Wild (1993) noted minor differences in coloration and the amount of

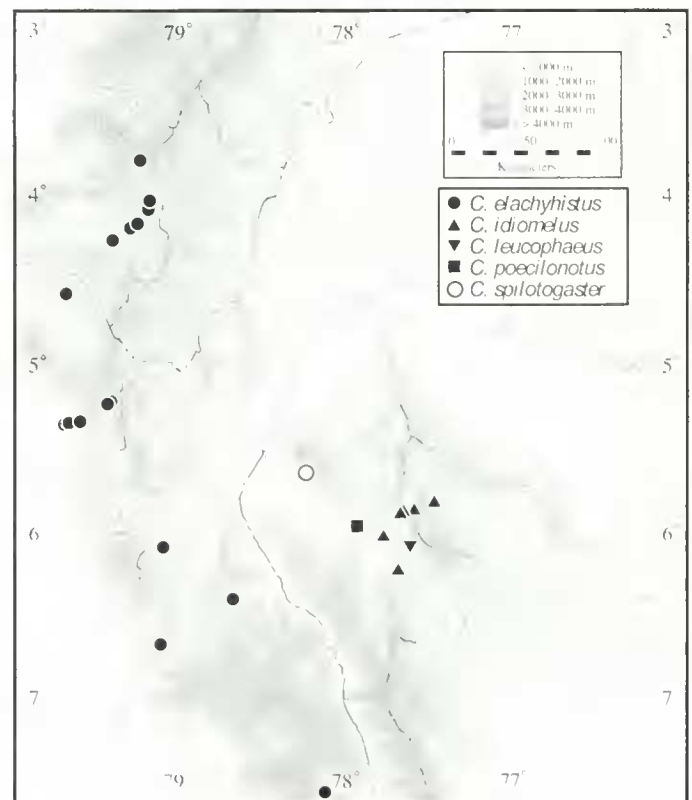


Fig. 10. Localities of occurrence of five species of *Colostethus*.

webbing between specimens from those localities and those from the Loja Basin in Ecuador. Comparison of specimens from nine localities in northwestern Peru reveals minor differences in SVL and different proportions of individuals that have a pair of brown spots on the gular-chest region or of females that have a mottled abdomen (Table 5). However, specimens from all of these localities are consistent in having a cream longitudinal stripe on the anterior surface of the thigh and a brown longitudinal on the upper arm. In some individuals from Huancabamba, the toe-webbing formula for Toe IV is 3*; in others it is 4* or 4. At all other Peruvian localities the formula for Toe IV is 4* to 4*.

Topotypic specimens from the vicinity of Loja, Provincia de Loja, Ecuador, and from other localities in southern Ecuador resemble those from northern Peru in having a cream longitudinal stripe on the anterior surface of the thigh and a brown longitudinal stripe on the upper arm, as well as a toe webbing for Toe IV as 4* to 4*. All have a pair of brown spots on the gular-chest region, and 52–91% of the females in four samples have a mottled abdomen (Table 5).

On the average, individuals of both sexes from Peru are smaller than those from Ecuador. Males from Ecuador have SVLs of 16.3–21.5 mm (\bar{x} = 19.1, N = 28), in contrast to 15.2–20.9 mm (\bar{x} = 17.7, N = 44) from Peru, whereas females from Ecuador have SVLs of 19.6–25.8 mm (\bar{x} = 22.6, N = 47), in contrast to 17.2–23.6 mm (\bar{x} = 21.1, N = 52) from Peru. Mean snout–vent lengths of females of 13 samples were regressed against elevations of their respective localities; the analysis revealed no significant correlation (P = 0.9452).

The variation in this species is further confounded by differences among tadpoles from separate sites. In contrast to the coloration of tadpoles described here, Duellman and Wild (1993) noted that living tadpoles from Huan-

cabamba, Departamento de Piura, Peru, had a dull brown body and a cream tail with a reddish-brown mid-lateral line proximally. Edwards (1971:153) described the color of preserved tadpoles from Loja, Provincia de Loja, Ecuador, as "black above, dark gray to black below, becoming pale gray anterior to eyes; papillae and lips unpigmented; caudal musculature creamy white with black reticulations concentrated into small blotches anteriorly on dorsal half of tail."

Taran Grant (pers. comm., 16 July 2004) found that sequences of Cytochrome *b* are 13% divergent between the sample from 4 km W of Llama, Departamento de Cajamarca, and those from 8.5 km E Canchaque, Departamento de Piura, and Ayabaca, Departamento de Piura, whereas the divergence is only 2% between the last two samples. Careful examination of the specimens from 4 km W Llama (KU 212518–24) reveals no consistent morphological differences from other populations of *Colostethus elachyhistus*, a nominal species that may include two or more cryptic biological species.

Colostethus eleutherodactylus new species

Holotype.—KU 211814, an adult female, from 16 km ESE of Shapaja (ca. 06°37' S, 76°15' W), 360 m, Provincia de San Martín, Departamento de San Martín, Peru; obtained on 19 February 1989 by John J. Wiens.

Paratype.—KU 211813, an adult male, collected with the holotype by Rainer Schulte.

Diagnosis.—A moderately small species of *Colostethus* with the following characteristics: (1) SVL in male 21.0 mm, 22.7 mm in female; (2) disc on Finger III greatly expanded; (3) Fingers I and II equal in length; (4) lateral fringes absent on fingers; (5) disc on Toe IV greatly expanded; (6) lateral fringes absent on toes; (7) outer tarsal fold present; curved

Table 5. Geographic variation in *Colostethus elachyhistus*. Localities arranged from north to south.

Locality	N	Male SVL (mm)	Female SVL (mm)	Females with mottled abdomen	Pair of brown spots on throat
Ecuador:					
San Lucas	7	17.4–21.4 (\bar{x} = 19.4, n = 2)	23.5–25.1 (\bar{x} = 24.2, n = 5)	60%	100%
Loja	45	17.2–21.5 (\bar{x} = 19.4, n = 20)	19.6–25.8 (\bar{x} = 22.8, n = 25)	52%	100%
Cariamanga	12	16.3–19.5 (\bar{x} = 18.1, n = 6)	20.4–23.0 (\bar{x} = 21.4, n = 6)	67%	100%
Macará	11	—	20.5–23.7 (\bar{x} = 21.9, n = 11)	91%	100%
Peru:					
Ayabaca	4	20.2, n = 1)	20.5–21.7 (\bar{x} = 21.2, n = 3)	33%	75%
Huancabamba	28	16.7–19.8 (\bar{x} = 18.4, n = 18)	20.2–23.4 (\bar{x} = 21.8, n = 10)		
Canchaque	8	16.8–19.3 (\bar{x} = 18.1, n = 2)	18.6–22.5 (\bar{x} = 20.7, n = 6)		
Abra de Porculla	32	15.2–18.7 (\bar{x} = 16.3, n = 17)	17.2–21.5 (\bar{x} = 19.7, n = 9)	11%	100%
Santa Cruz	7	—	21.4–22.7 (\bar{x} = 22.0, n = 7)	0%	86%
Cutervo	3	—	18.5–19.2 (\bar{x} = 18.9, n = 2)	67%	100%
Lamas	7	16.0, n = 1	20.2–22.8 (\bar{x} = 21.5, n = 6)	67%	71%
Cajabamba	9	19.3–20.9 (\bar{x} = 20.1, n = 3)	20.9–23.6 (\bar{x} = 21.9, n = 6)	33%	89%

inner tarsal fold on distal half of tarsus; (8) webbing absent between toes; (9) dorsolateral stripe present; (10) short oblique lateral stripe present; (11) ventrolateral stripe absent; (12) gular-chest region uniformly creamy white; (13) abdomen creamy white; (14) no sexual dimorphism in coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

In northern Peru and Ecuador, *Colostethus exasperatus* is the only other member of the genus that has Fingers I and II equal in length and possesses dorsolateral and oblique lateral stripes; it differs from *C. eleutherodactylus* by having a swollen black gland on the inner surface of the elbow, having dark marbling laterally on the belly, and by lacking an outer tarsal fold. *Colostethus sordidatus*, *C. idiomelus*, and *C. sylvaticus* also have the Fingers I and II equal in length; *C. sordidatus* lacks a dorsolateral stripe, and the other two lack oblique lateral stripes. Furthermore, *C. idiomelus* and *C. sylvaticus* have only slightly expanded discs on the digits, and both have lateral fringes on the fingers and toes. The coloration of *C. eleutherodactylus* is much like that of *C. nexipus*, a species that has Finger I shorter than Finger II, distinct lateral fringes on the digits, and toes about half webbed. The coloration also resembles that of *C. patitae* in the Serranía de Sira in central Peru; that species differs from *C. eleutherodactylus* by having Finger I shorter than Finger II, a bright yellow dorsolateral stripe, and dark brown upper lip in contrast to the yellowish tan upper lip in *C. eleutherodactylus* (Lötters et al., 2003).

Description.—($N = 2$: 1 male, 1 female). Body moderately robust; head slightly longer than wide; head length 33.9% and 35.2% ($\bar{x} = 34.6\%$) of SVL; head width 32.2% and 34.3% ($\bar{x} = 33.3\%$) of SVL; snout long, nearly truncate in dorsal view, bluntly rounded in profile; loreal region barely concave; nostrils protuberant laterally, anterior edges at level of anterior margin of lower jaw; eye–nostril distance 67.7% of eye length; supratympanic bulge diffuse, obscuring upper edge of tympanum; length of tympanum 51.6% length of eye in male, 64.5% in female, separated from eye by distance about one-fourth length of eye.

Forelimb moderately long, slender; Fingers I and II equal in length; fingers unwebbed, lacking lateral fringes; Finger III not swollen in male; terminal discs expanded, nearly truncate, about twice width of penultimate phalanges; subarticular tubercles prominent, subconical; supernumerary tubercles absent; palmar tubercle large, elevated, nearly round; thenar tubercle elevated, bluntly ovoid; nuptial excrescences absent. Hind limb moderately robust, short; tibia length 45.4% and 47.6% ($\bar{x} = 46.5\%$) SVL; foot length 43.6% and 45.7% ($\bar{x} = 44.7\%$) SVL; outer tarsal fold low, thin, extending full length of tarsus; inner tarsal fold low, a shallow sigmoid curve from prominent tarsal tubercle to elliptical inner metatarsal tubercle; outer metatarsal tubercle subconical; toes unwebbed,

lacking lateral fringes; terminal discs expanded, about twice width of penultimate phalanges; subarticular tubercles prominent, subconical; supernumerary tubercles absent.

Skin on dorsum of body and hind limbs smooth; skin on flanks finely shagreen; skin of ventral surfaces smooth; cloacal opening directed posteroventrally near upper level of thighs; cloacal sheath short. Tongue elongate, widest posteriorly, not notched behind, free posteriorly for about two-thirds of its length; median lingual process absent.

Color in preservative: Dorsum of head and body brown; flanks dark brown; dark brown stripe across snout, through loreal and tympanic regions, confluent with brown flanks; dorsolateral stripe tan, continuous across snout, canthal region, outer edge of upper eyelid to point above insertion of hind limb; oblique lateral stripe white, extending from groin to midflank, fragmented; ventrolateral stripe absent; dorsal surfaces of upper arm creamy tan; anterior and posterior surfaces of upper arm brown; forearm tan with brown transverse bars; dorsal surfaces of hind limbs brown with dark brown transverse bars; anterior surfaces of thighs brown with diagonal cream mark proximally; posterior surfaces of thighs brown with tan flecks; upper lip creamy tan. Venter creamy tan with minute brown flecks on throat and chest; palmar surfaces creamy tan; plantar surfaces brown.

Color in life: Dorsum brown with dark brown markings; dorsolateral stripe tan with orange tint on head; flanks black with broken creamy white oblique lateral stripe; thighs and upper arms pale dull yellow with brown markings; dorsal surfaces of digital scutes white, contrasting with adjacent brown surfaces; venter dull yellow; iris pale copper (Fig. 5E).

Measurements of holotype (in mm): SVL 22.7; tibia length 10.3; foot length 9.9; head width 7.3; head length 7.7; eye–nostril distance 2.1; length of eye 3.1; length of tympanum 2.0.

Tadpoles.—An adult male with a SVL of 21.0 mm was carrying five tadpoles. Five back-riding tadpoles (KU 215593) have body lengths of 3.8–4.3 mm ($\bar{x} = 4.04$) and total lengths of 10.8–11.2 mm ($\bar{x} = 10.9$). The tadpoles are in Stage 25; the intestines do not seem to be fully differentiated, and the body cavity is filled with yolk. All individuals have thin jaw sheaths and variable development of labial tooth rows; two have LTRF of 1/0, two have 2/1, and one has 2/2. In preservative, the dorsal and lateral surfaces of the body are brown; the caudal musculature is creamy white with taint brown spots above the midline, and the fins are translucent.

Distribution and ecology.—This species is known only from the type locality at an elevation of 360 m in disturbed humid tropical forest just north of the Río Huallaga in the uppermost reaches of the Amazon Basin (Fig. 8). Both in-

dividuals were active in leaf litter near a small stream in a rocky ravine by day.

Etymology.—The specific name is a compound adjective derived from the Greek *eleutheros* meaning free and the Greek *daktylos* meaning toe. The name refers to the unwebbed toes of this species.

Colostethus idiomelus Rivero

Colostethus idiomelus Rivero, 1991a:10. Holotype: MCZ A-100260 from Venceremos, Departamento de San Martín, Peru, 1620 m.

Diagnosis.—A moderate-sized species of *Colostethus* with the following characteristics: (1) maximum SVL of males 24.8 mm, of females 27.8 mm; (2) disc on Finger III not expanded; (3) Fingers I and II equal in length; (4) narrow lateral fringes present on fingers; (5) disc on Toe IV slightly expanded; (6) narrow lateral fringes present on toes; (7) curved inner tarsal fold on distal half of tarsus; (8) webbing absent between toes; (9) dorso-lateral stripe present; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) gular-chest region with pair of brown spots; (13) abdomen mottled gray and white anteriorly, yellow posteriorly; (14) no sexual dimorphism in ventral coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

Three other species in Ecuador and Peru have dorso-lateral stripes and Fingers I and II equal in length. Of these, *Colostethus eleutherodactylus* and *C. exasperatus* also have oblique lateral stripes and expanded discs on the digits (oblique stripe absent and discs on fingers not expanded in *C. idiomelus*). *Colostethus sylvaticus* is most like *C. idiomelus* in having the first and second fingers equal in length, weakly expanded discs on the digits, no oblique lateral stripe, and a pair of dark spots on the throat; however, *C. sylvaticus* differs from *C. idiomelus* by having more extensive lateral fringes on the fingers and toes, much broader dorso-lateral stripe, more dark bars on the hind limbs (3 or 4 bars vs. 2), and a yellow throat in life. Also, *C. sylvaticus* is slightly larger (Table 1).

Description.—($N = 61$: 38 males, 23 females). SVL 19.5–24.8 mm ($\bar{x} = 22.0$) in males, 23.0–27.8 mm ($\bar{x} = 25.1$) in females; body robust; head slightly longer than wide; head length 33.9–39.9% ($\bar{x} = 36.6\%$) of SVL; head width 32.3–41.4% ($\bar{x} = 34.4\%$) of SVL; snout moderately long, rounded in dorsal view, bluntly rounded in profile; loreal region flat; nostrils barely protuberant laterally, anterior edge just posterior to level of anterior margin of lower jaw; eye–nostril distance 60.0–83.3% ($\bar{x} = 70.4\%$) of length of eye; supratympanic bulge distinct, angular posterodorsal to tympanum, obscuring dorsal edge and upper posterior edge of tympanum; length of tympanum 57.1–72.4% ($\bar{x} = 63.3\%$) length of eye, separated from eye by distance about one-fifth length of eye.

Forelimb moderately short, robust; Fingers I and II equal in length; fingers unwebbed, bearing narrow, keel-like lateral fringes; terminal disc not expanded; subarticular tubercles small, rounded; supernumerary tubercles absent; palmar tubercle large, round; thenar tubercle small, elliptical. Hind limb short, robust; foot longer than tibia; tibia length 39.9–52.5% ($\bar{x} = 48.1\%$) SVL; foot length 40.4–52.0% ($\bar{x} = 47.2\%$) SVL; outer tarsal fold absent; inner tarsal fold elevated, shallow sigmoid on distal third of tarsus; inner metatarsal tubercle small, elliptical; outer metatarsal tubercle subconical, nearly as large as inner tubercle; toes unwebbed, bearing narrow keel-like lateral fringes; terminal discs slightly expanded; subarticular tubercles small, rounded; supernumerary tubercles absent.

Skin on dorsum smooth to shagreen, usually with scattered small tubercles postsacrally on dorsum; skin on flanks shagreen to finely granular; skin on venter smooth; cloacal opening directed posteriorly at upper level of thighs; cloacal sheath short. Tongue elongate, slightly widest and shallowly indented posteriorly, free behind for about half of its length; median lingual process absent.

Color in preservative: Dorsum of head and body dull tan with dark brown markings consisting of (1) irregular interorbital mark, V-shaped marks in occipital and scapular regions, and pair of longitudinal postsacral marks (68.3%); (2) small interorbital spot or longitudinal mark, pair of diagonal marks in scapular region with small spots posteriorly, pair of longitudinal postsacral marks (15.0%); (3) pair of diagonal marks or V-shaped mark in occipital region; rest of dorsum with many small spots (11.7%); dorsum of head and body plain or only with a pair of longitudinal dark postsacral marks (5.0%) flanks brown, gray below in some individuals; narrow, dark stripe across snout, through loreal and supratympanic regions, to midflank; dorso-lateral stripe tan, narrow across snout and along outer edge of upper eyelid, usually widest and commonly bordered by black on body; oblique lateral stripe and ventrolateral stripes absent. Forelimb tan with one or two narrow brown transverse bars on dorsal surface of forearm; brown streak proximally on lateral surface of upper arm; dorsal surfaces of hind limbs dull tan with faint transverse brown bars—one or two on thigh, three on shank, one or two on foot; anterior surfaces of thighs dark brown; posterior surfaces of thighs pale brown with vertical dark brown extensions of bars on dorsal surfaces. Side of face and upper lip tan; cream stripe on posterior part of upper jaw; venter creamy tan with faint brown mottling anterior to midlength of abdomen; pair of diffuse brown spots posterolaterally on throat; palmar and plantar surfaces brown or tan.

Color in life: Dorsum dull tan to rich orange-brown, to grayish tan with green tint in some places; dorsal markings olive-brown to black (Figs. 5F and G); dorso-lateral stripe pinkish tan, yellowish orange or cream, usually

Table 6. Measurements (in mm) of transporting males and back-riding tadpoles of *Colostethus idiomelus*. Range of variation followed by mean in parentheses).

Male SVL	N	Body length	Total length
20.5	7	4.3–4.4 (\bar{x} = 4.39)	9.8–10.5 (\bar{x} = 10.31)
20.7	12	4.1–4.5 (\bar{x} = 4.29)	10.2–11.8 (\bar{x} = 11.04)
23.8	10	3.7–3.9 (\bar{x} = 3.76)	10.2–10.4 (\bar{x} = 10.29)

bordered by dark brown; flanks tan to gray; labial stripe pinkish cream; anterior and posterior surfaces of thighs yellow to dull orange; digital scutes gray; iris dull bronze. Throat, chest, and anterior part of abdomen white with dark brown or gray mottling, yellow suffusion on anterior part of throat; posterior part of belly and ventral surfaces of hind limbs yellow; ventral surfaces of forelimbs dull yellow (Fig. 511).

Tadpoles.—Males transporting 7–12 tadpoles each were found in January and February (Table 6). The intestines of back-riding tadpoles contain yolk. The tadpoles probably grow and begin developing keratinized jaw sheaths and labial teeth while being transported. Thin jaw sheaths are present in some of the smallest tadpoles (body lengths of 3.7–3.8 mm); two tadpoles with body lengths of 4.4 mm have LTRFs of 0/1, one of the same size has an LTRF of 0/2, and one with a body length of 4.5 mm has an LTRF of 0/3. Anterior tooth rows apparently develop after the tadpoles are free-swimming, the smallest individual of which as a body length of 6.7 mm and an LTRF of 2/3.

Free-swimming tadpoles in various stages of development were found in January and February in slow-moving, even marshy, streams (Table 7). These are associated with *Colostethus idiomelus* because adults of that species were found at three of the four localities where tadpoles were collected, and *C. idiomelus* is the only species of *Colostethus* known to occur at two of those localities. Furthermore, a tadpole in Stage 43 has a well-defined dorsolateral stripe as in adults, and recently metamorphosed young with SVLs of 10.8–14.1 mm have the incipient color pattern of the adults.

A typical tadpole (KU 215607) in Stage 34 has a body length of 14.2 mm and a total length of 34.7 mm; body wider (9.3 mm) than high (7.2 mm); snout bluntly rounded in dorsal view, sloping anteroventrally from level of orbits to rounded tip in profile; external nares small, about midway between snout and orbits; eye small (1.4 mm) situated dorsally, directed dorsolaterally, not visible from below; interorbital distance 3.5 mm; spiracle sinistral; tube short, attached to body for its entire length; spiracular opening directed posterodorsally just below midline at about midlength of body; cloacal tube short, dextral, attached to ventral fin. Caudal musculature moderately

Table 7. Measurements (in mm) of free-swimming tadpoles of *Colostethus idiomelus*. Range of variation followed by mean in parentheses.

Stage	N	Body length	Total length
25	23	8.4–13.5 (\bar{x} = 10.64)	16.9–35.6 (\bar{x} = 29.10)
28	5	12.2–13.1 (\bar{x} = 12.50)	32.2–35.3 (\bar{x} = 33.48)
29	5	13.0–14.2 (\bar{x} = 13.66)	33.2–39.0 (\bar{x} = 35.10)
34	2	14.2–14.3 (\bar{x} = 14.25)	34.7–35.5 (\bar{x} = 35.10)
35	2	14.0–14.1 (\bar{x} = 14.05)	36.8–37.0 (\bar{x} = 36.90)
36	4	14.6–15.5 (\bar{x} = 14.98)	36.0–38.5 (\bar{x} = 37.93)
40	3	15.0–16.2 (\bar{x} = 15.53)	36.9–42.6 (\bar{x} = 39.90)
43	1	16.3	36.6

robust, approximately uniform in depth on anterior third of tail, gradually diminishing distally to pointed tip; dorsal fin originating on base of caudal musculature, gradually increasing in height on proximal two thirds of tail, and declining posteriorly to an acutely rounded tip; ventral fin originating on body wall, highest at midlength of tail, where equal in height to caudal musculature, noticeably less than height of dorsal fin (Fig. 9C).

Oral disc 3.9 mm wide, directed anteroventrally; deep lateral folds in labia; median half of anterior labium bare; elsewhere labia with single irregular row of small, subconical marginal papillae; submarginal papillae absent; few rounded papillae in lateral folds. Jaw sheaths thin, finely serrate; anterior sheath in form of broad arch; posterior sheath broadly V-shaped; LTRF 2/3; all rows of teeth about equal in length,

In life, body olive-brown; belly creamy gray; tail tan with olive flecks and brown spots or reticulations; it is tan to bronze. In preservative, dorsum and sides of body dark brown; belly gray; caudal musculature tan with midlateral brown streak on proximal third of musculature; caudal fins translucent with brown reticulations, most numerous and minute white flecks on fins and musculature on distal third of tail (Fig. 9C).

Distribution and ecology.—*Colostethus idiomelus* is known from several localities at elevations of 1620–2200 m and two localities at 2280 m and 2840 m in humid montane forest in the northern part of the Cordillera Central in Peru (Fig. 10). Individuals were found in spring seepages and along small streams. At a site at 2180 m on the east slope of Abra Pardo Miguel, *C. idiomelus* occurs sympatrically with the slightly larger *C. aeruginosus*, and at a site at 1620 m, it occurs sympatrically with *C. mittermeieri*.

Remarks.—The original description of *Colostethus idiomelus* was based on a single subadult female, not an adult female as stated by Rivero (1991a).

Colostethus insulatus new species

Holotype.—KU 211857, an adult female, from 17 km ENE (by road) of Balsas (ca. 06°50' S, 77°56' W), 1810 m, Provincia de Chachapoyas, Departamento de Amazonas,

Peru; one of a series collected by Fernando M. Cuadros and John J. Wiens on 21 January 1989.

Paratopotypes.—KU 211858–70, 2 adult males, 11 adult females; same collectors and date.

Referred specimens.—See Appendix 1.

Diagnosis.—A moderately small species of *Colostethus* with the following characteristics: (1) maximum SVL of males 22.2 mm, of females 26.0 mm; (2) disc on Finger III expanded, half again width of penultimate phalange; (3) Finger I longer than Finger II, (4) lateral fringes present on fingers; (5) disc on Toe IV expanded, half again width of penultimate phalange; (6) lateral fringes present on toes; (7) outer tarsal fold and tarsal tubercle absent; inner tarsal fold curved, distinct on distal half of tarsus; (8) toes webbed basally; (9) dorsolateral stripe absent; (10) oblique lateral stripe present; (11) ventrolateral stripe absent; (12) gular-chest region cream with pair of brown spots laterally on throat; (13) abdomen cream; (14) no sexual dimorphism in coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

Few species of *Colostethus* in Ecuador and Peru have Finger I longer than Finger II and an oblique lateral stripe. Of these, *C. argyrogaster* differs from *C. insulatus* by having a pale ventrolateral stripe, orange inguinal region in life, no fringes on the digits, and basal webbing only between Toes III and IV. *Colostethus leucophaeus* differs by having the toes about one-half webbed and the oblique lateral stripe present only in the groin, whereas *C. pulcherrimus* differs by having black flanks with pale blue flecks. *Colostethus fugax* and *C. machalilla* differ by having Finger III swollen in males and by lacking fringes on the digits and discrete dark marks in the gular-chest region. The larger *C. toachi* also lacks fringes on the digits and has a pale ventrolateral stripe, as does *C. melanolaemus*, in which the oblique lateral stripe is diffuse. Other species that have Finger I longer than Finger II in the region include *C. conspicuus*, *kingsburyi*, *ornatus*, and *talamancae*, all of which have dorsolateral stripes, and all except *C. talamancae* lack fringes on the digits. *Colostethus aeruginosus* and *C. mittermeieri* also have Finger I longer than Finger II, but they lack all longitudinal stripes.

Description.—($N = 32$: 9 males, 22 females, 1 juvenile). SVL 17.2–22.2 ($\bar{x} = 19.7$) mm in males, 20.2–26.0 ($\bar{x} = 22.8$) mm in females; body robust; head about as wide as long; head length 33.3–43.6% ($\bar{x} = 34.9\%$) of SVL; head width 32.5–40.2% ($\bar{x} = 34.9\%$) of SVL; snout moderately long, bluntly rounded in dorsal view, rounded in profile; loreal region slightly concave; nostrils barely protuberant laterally, anterior margins slightly posterior to level of anterior margin of lower jaw; eye–nostril distance 58.6–72.7% ($\bar{x} = 64.6\%$) of length of eye; supratympanic bulge weak, barely covering upper and posterodorsal edge of tympanum;

otherwise, tympanic annulus distinct; length of tympanum 46.4–58.6% ($\bar{x} = 50.6\%$) of length of eye, separated from eye by distance less than one-fourth length of eye.

Forelimb moderately long, robust; Finger I slightly longer than Finger II; fingers not webbed, bearing narrow lateral fringes; Finger III in males not swollen; terminal discs expanded, about half again width of penultimate phalanges; subarticular tubercles moderately large, subconical; supernumerary tubercles absent; palmar tubercle large, round; thenar tubercle small, elongately elliptical; nuptial excrescences absent. Hind limb short, robust; tibia length 42.9–48.2% ($\bar{x} = 45.6\%$) SVL; foot length 41.0–48.0% ($\bar{x} = 44.6\%$) SVL; outer tarsal fold absent; inner tarsal fold curved from low tubercle at midlength of tarsus to elliptical inner metatarsal tubercle; outer metatarsal tubercle subconical; toes webbed basally; webbing formula $12-2-112-3113-4-1V4-3V$; lateral fringes present on toes; terminal discs expanded, about half again width of penultimate phalanges; subarticular tubercles small, round; supernumerary tubercles absent.

Skin on dorsum of body and hind limbs, flanks, and venter smooth; cloacal opening directed posteriorly at upper level of thighs; cloacal sheath long. Tongue long, widest and shallowly notched posteriorly, free behind for about half of its length; median lingual process absent.

Color in preservative: Dorsum of head and body brown with small, irregular, dark brown spots, principally on body; dark brown stripe across tip of snout through loreal and tympanic regions to anterior part of flanks; midflank gray; groin tan. Dorsolateral and ventrolateral stripes absent; oblique lateral stripe, creamy white, distinct from groin to posterior part of upper eyelid. Forelimb pale tan, with or without irregular brown marks on forearm; dorsal surfaces of hind limbs brown, usually with darker brown transverse bars—two each on thigh, shank, and foot; anterior surfaces of thighs brown with cream longitudinal stripe on at least proximal half of thigh, continuous with oblique lateral stripe, diffuse or indistinct in some specimens; posterior surfaces of thighs brown with or without diffuse darker brown mottling; upper lip pale tan, usually with faint brown mottling. Venter cream with pair of diffuse brown or grayish brown spots posterolaterally on throat; palmar and plantar surfaces pale brown; webbing translucent.

Color in life: Dorsum reddish brown with dark brown middorsal marks, anterior two or three of which broadly chevron-shaped, posterior two usually round, quadrangular, or elongate; upper lip and proximal dorsal surfaces of upper arm white; rest of forearm brown with diffuse grayish-white mottling; oblique lateral stripe creamy white; flanks gray mottled with brown; dorsal surfaces of thighs dull brown with darker brown markings ranging from irregular spots to transverse bars; anterior surfaces

of thighs brown with narrow creamy-white longitudinal stripe connected to oblique lateral stripe in groin; throat gray with pair of black spots; belly creamy white; ventral surfaces of hind limbs pale gray with diffuse, dull orange spot on proximal ventral surface of shank; digital scutes white to pale gray in contrast to brown digits; iris bronze with black flecks (Figs. 5D and 6A).

Measurements of holotype (in mm): SVL 22.0; tibia length 9.9; foot length 9.6; head width 7.8; head length 7.9; eye–nostril distance 2.0; length of eye 2.9; length of tympanum 1.7.

Tadpoles.—Tadpoles were collected at three of the localities where adults were found; because only one species of *Colostethus* was found at each of these sites and because metamorphosing young are like the adults, these tadpoles are assigned to *Colostethus insulatus*. Tadpoles in various stages of development were found in a rocky pool at the base of a waterfall, in a small pool in a seepage area, and in a small spring-fed pool (Table 8).

A typical tadpole (KU 215600) in Stage 34 has a body length of 13.0 mm and a total length of 38.8 mm; body globular, wider (9.6 mm) than high (7.0 mm); snout rounded in dorsal view and in profile; nares directed dorsolaterally about midway between tip of snout and orbits; eyes moderately large (1.7 mm), situated and directed dorso-laterally, not visible from below; interorbital distance 3.2 mm; spiracle sinistral, short, attached for its entire length to body wall; spiracular opening directed posterodorsally well below midline at about midlength of body; cloacal tube short, dextral, attached to ventral fin. Caudal musculature robust, being equal in height throughout proximal half of tail, diminishing gradually to pointed terminus; dorsal fin originating on base of caudal musculature, reaching greatest height at about midlength of tail, diminishing to bluntly rounded tip; ventral fin originating on body wall, reaching greatest height just posterior to midlength of tail, where dorsal and ventral fins equal in height, and slightly more than height of caudal musculature (Fig. 9D).

Oral disc 3.8 mm wide, directed anterolaterally; median half of anterior labium bare; elsewhere labia bearing single row of slender, pointed marginal papillae; submarginal papillae absent; labia infolded laterally; few small, round papillae in folds. Jaw sheaths moderately slender, coarsely serrate; anterior sheath forming broad arch; lower sheath broadly V-shaped; LTRF 2(1)/3; A_3 longest; P_3 shortest; other rows equal in length.

In preservative, dorsum and sides of body dark brown; belly translucent; caudal musculature tan with fine brown reticulations; caudal fins translucent with brown flecks on dorsal fin (Fig. 9D). In life, body olive-brown; tail brown with olive flecks; iris pale bronze. Recently metamorphosed young colored like adults, except slightly paler and lacking dark spots on throat.

Table 8. Measurements (in mm) of free-swimming tadpoles of *Colostethus insulatus*. Range of variation followed by mean in parentheses.

Stage	N	Body length	Total length
25	12	5.4–9.7 (\bar{x} = 7.83)	11.6–25.1 (\bar{x} = 19.36)
29	1	10.2	23.3
31	1	10.4	23.6
32	1	11.3	28.4
34	3	12.5–13.5 (\bar{x} = 13.00)	35.5–38.8 (\bar{x} = 37.30)
37	1	15.0	41.5
41	1	14.2	39.2
43	1	14.3	34.3
44	1	14.3	24.2
46	3	14.2–14.8 (\bar{x} = 14.43)	—

Distribution and ecology.—*Colostethus insulatus* inhabits the middle Río Marañón Valley in northern Peru, where it is known from elevations of 1260–2600 m (Fig. 4). This region supports dry scrub forest, which in some areas is dominated by cacti. A few small streams cascade down the steep slopes from the adjacent highlands of the Cordillera Occidental and Cordillera Central. *Colostethus* were found by day on and under rocks adjacent to streams and especially in spray zones of waterfalls; others were under rocks in seepage areas or adjacent to small spring-fed streams. Tadpoles were found in quiet pools.

Etymology.—The specific name, *insulatus*, is Latin meaning isolated and refers to the disparate mesic environments inhabited by this species in otherwise inhospitable terrain.

Remarks.—One male (SVL 18.3 mm) and nine females (SVLs 20.2–24.9 mm; \bar{x} = 22.8) from 2 km NW of San Juan, 2290 m, Departamento de Cajamarca, resemble typical *Colostethus insulatus* in size and structure, but differ somewhat in coloration. The dorsum is dull olive-gray with brown markings; the oblique lateral stripe is pale orange-tan (Fig. 5D). The flanks are gray with cream spots, and the venter is dull creamy white with a pair of diffuse brown spots on the throat. This sample is from the headwaters of the drainage of the Río Cajamarca, which flows into the Río Marañón.

Colostethus leucophaeus new species

Holotype.—KU 211879, an adult female, from Molinapampa (06°11' S, 77°38' W, 2400 m), Provincia de Chachapoyas, Departamento de Amazonas, Peru; one of a series collected by William E. Duellman and Michael E. Morrison on 26 January 1989.

Paratypes.—KU 211880–83 and MHNSM 6215–17 collected with the holotype.

Diagnosis.—A moderate-sized *Colostethus* with the following characteristics: (1) maximum SVL of males 25.2 mm, of females 26.1 mm; (2) disc on Finger III expanded,

slightly wider than penultimate phalange; (3) Finger I longer than Finger II; (4) lateral fringes present on fingers; (5) disc on Toe IV expanded, slightly wider than penultimate phalange; (6) lateral fringes present on toes; (7) outer tarsal fold and tarsal tubercle absent; inner tarsal fold curved, distinct on distal two-thirds of tarsus; (8) toes about one-half webbed; (9) dorsolateral stripe absent; (10) oblique lateral stripe present posteriorly; (11) ventrolateral stripe absent; (12) gular-chest region cream; (13) abdomen cream; (14) no sexual dimorphism in coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

Only a few species in Ecuador and northern Peru have Finger I longer than Finger II, an oblique lateral stripe, and no dorsolateral stripe. Of these, *C. argyrogaster* differs from *C. leucophaeus* by having a pale ventrolateral stripe, orange inguinal region in life, no fringes on the digits, and basal webbing only between Toes III and IV. *Colostethus pulcherrimus* differs by having black flanks with pale blue flecks. *Colostethus fugax* and *C. machalilla* differ by having Finger III swollen in males and by lacking fringes on the digits. The equally large *C. toachi* also lacks fringes on the digits and has a pale ventrolateral stripe, as does *C. melanolaemus*, in which the oblique lateral stripe is diffuse. Four other species have the toes at least one-half webbed; these are *C. fuliginosus*, *nexipus*, *peculiaris*, and *sordidatus*. Fingers I and II are equal in length in *C. sordidatus*, Finger I is shorter than Finger II in *C. fuliginosus*, *nexipus*, and *peculiaris*.

Description.—($N = 8$: 3 males, 2 females, 3 juveniles). SVL 24.7–25.2 mm ($\bar{x} = 25.0$) in males, 23.7–26.1 mm ($\bar{x} = 24.9$) mm in females; body robust; head slightly longer than wide; head length 34.9–36.0% ($\bar{x} = 35.3\%$) of SVL; head width 34.1–35.2% ($\bar{x} = 34.7\%$) of SVL; snout moderately short, bluntly rounded in dorsal view and in profile; loreal region slightly concave; nostrils barely protuberant laterally, anterior margins slightly posterior to level of anterior margin of lower jaw; eye–nostril distance 62.5–63.3% ($\bar{x} = 62.7\%$) of length of eye; supratympanic bulge weak, barely covering upper and posterodorsal edge of tympanum; otherwise, tympanic annulus distinct; length of tympanum 53.1–56.2% ($\bar{x} = 54.4\%$) of length of eye, separated from eye by distance about one-third length of eye.

Forelimb moderately long, slender; Finger I much longer than Finger II; fingers not webbed, bearing broad lateral fringes; Finger III not swollen in males; terminal discs expanded, slightly wider than penultimate phalanges; subarticular tubercles moderately small, low, rounded; supernumerary tubercles absent; palmar tubercle large, round; thenar tubercle small, ovoid; nuptial excrescences absent. Hind limb short, robust; tibia length 40.9–44.1% ($\bar{x} = 42.4\%$) of SVL; foot length 42.9–49.0% ($\bar{x} = 45.0\%$) of SVL; outer tarsal fold absent; inner tarsal fold elevated, curved on distal two thirds of tarsus to small, elliptical

inner metatarsal tubercle; outer metatarsal tubercle subconical; toes slightly more than one-half webbed; webbing formula $\text{II}^+ - 2\text{III}^+ - 3 \text{III}2 - 3 \text{IV}3 - 1 \text{V}$; lateral fringes present on toes; terminal discs expanded, wider than penultimate phalanges; subarticular tubercles small, low, round; supernumerary tubercles absent.

Skin on dorsum of body and hind limbs, and venter smooth; skin on flanks finely shagreen; cloacal opening directed posteriorly at upper level of thighs; cloacal sheath short. Tongue long, widest and shallowly notched posteriorly, free behind for about half of its length; median lingual process absent.

Color in preservative Dorsum of head, body, and limbs dull brown with small, faint, irregular dark brown spots on body; diffuse dark brown stripe across tip of snout, through loreal and supratympanic regions, present or not on anterior part of flanks; otherwise flanks grayish brown. Dorsolateral and ventrolateral stripes absent; oblique lateral stripe creamy white, present only in groin. Forelimb brown with darker brown irregular marks on forearm; anterior surface of upper arm tan with brown longitudinal stripe; dorsal surfaces of hind limbs brown with darker brown transverse bars—three or four each on thigh, shank, and foot; anterior surfaces of thighs creamy tan with continuation of transverse brown bars; posterior surfaces of thighs creamy tan with dark brown longitudinal stripe on posteroventral surfaces; upper lip and tympanic region pale tan. Venter cream with fine melanophores on throat; palmar and plantar surfaces brown; webbing cream.

Three juveniles having SVLs of 18.5–19.8 mm ($\bar{x} = 19.3$) are colored like the adults. However, the pattern on the dorsal surfaces of the hind limbs is more striking; the interspaces between the dark brown transverse bars are creamy tan.

Color in life: Dorsum dull grayish brown; flanks pale grayish brown; limbs, including digital scutes, dull brown with dark brown transverse bars; canthal and supratympanic stripes brownish black; short, dull cream oblique lateral stripe in groin; faint, pale gray line along posterior surfaces of thighs; belly dirty white; throat and ventral surfaces of limbs tinged with dull yellow; iris dull brown (Fig. 6B).

Measurements of holotype (in mm) SVL 26.1, tibia length 11.5, foot length 12.8, head width 9.0, head length 9.0, eye–nostril distance 2.0, length of eye 3.2, length of tympanum 1.7.

Tadpoles.—A small series of tadpoles, mostly in later stages of development, was obtained from a slow-moving, marshy stream in a pasture at the type locality. These tadpoles are associated with *Colostethus leucophaeus* because it is the only species of the genus known from the locality and because the metamorphosing tadpoles closely resemble the adults in coloration. The tadpoles are much larger than those of other species in northern Peru (Table 9).

Table 9. Measurements (in mm) of free-swimming tadpoles of *Colostethus leucophaeus*. Range of variation followed line by mean in parentheses.

Stage	N	Body length	Total length
28	1	15.6	37.5
32	1	20.0	45.0
40	1	20.5	50.2
43	1	18.7	48.5
44	2	18.8	28.2–34.1 (\bar{x} = 31.15)

A typical tadpole (KU 215603) in Stage 28 has a body length of 15.6 mm and a total length of 37.5 mm; body ovoid, slightly wider (9.5 mm) than high (8.6 mm); snout in dorsal view bluntly rounded, nearly truncate, rounded in profile; nares directed dorsolaterally about midway between tip of snout and orbits; eyes moderately small (1.6 mm), situated and directed dorsolaterally, not visible from below; interorbital distance 4.4 mm; spiracle sinistral, tube short, attached to body wall; sinistral opening directed posterodorsally well below midline at about midlength of body; cloacal tube short, dextral, attached to ventral fin. Caudal musculature, gradually diminishing from body to acutely rounded terminus; dorsal fin originating on anterior margin of caudal musculature, highest at about two-thirds of tail length, gradually diminishing to bluntly rounded tip; ventral fin originating on body wall, highest at about three-fourths of tail length; at midlength of tail, dorsal fin lower than ventral fin, neither as high as caudal musculature (Fig. 9E).

Oral disc 3.9 mm wide, directed anteroventrally; median two thirds of anterior labium bare; rest of labium bearing short, blunt marginal papillae; two rows of papillae in lateral folds; elsewhere, one row of papillae; submarginal papillae absent. Jaw sheaths moderately robust, serrated; anterior sheath in form of broad arch; posterior sheath widely V-shaped; LTRF 2(1)/3; all rows about equal in length.

In preservative, dorsum and sides of body dark brown; belly dark grayish brown; caudal musculature tan, becoming gray on distal third; fins brown (Fig. 9E). In life, body and tail dark gray.

Distribution and ecology.—This species is known only from the type locality at an elevation of 2400 m in the northern part of the Cordillera Central in Departamento de Amazonas, Peru (Fig. 10). The type series and the tadpoles were found amid water cress-like plants in a slow-moving, marshy stream in a pasture by day. In the same marshy stream, adults, metamorphosing young, and tadpoles of *Gastrotheca monticola* and *Scinax oreites* were found.

Etymology.—The specific name is a Latin adjective meaning ash-colored and refers to the generally dull gray appearance of this nondescript frog.

Colostethus mittermeieri Rivero

Colostethus mittermeieri Rivero, 1991a:3. Holotype: MCZ A-100217 from Venceremos, Departamento de San Martín, Peru, 1620 m.

Diagnosis.—A moderately large species of *Colostethus* with the following characteristics: (1) SVL in males to 27.2 mm, in females 28.2 mm; (2) disc on Finger III expanded, about half again width of penultimate phalange; (3) Finger I longer than Finger II; (4) lateral fringes present on fingers; (5) disc on Toe IV expanded, about half again width of the penultimate phalange; (6) lateral fringes present on toes; (7) curved inner tarsal fold on distal half of tarsus; (8) toes about one-fourth webbed; (9) dorsolateral stripe absent; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) gular-chest area with paired brown spots; (13) abdomen mottled anteriorly; (14) no sexual dimorphism in ventral coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

The only other species in Ecuador and Peru with Finger I longer than Finger II and lacking longitudinal stripes is *Colostethus aeruginosus*; this species differs from *C. mittermeieri* by having unwebbed toes and a dark venter with pale spots.

Description.—($N = 2$: 1 male, 1 female). Body moderately robust; head longer than wide; head length 35.1 and 37.7% ($\bar{x} = 36.4$) of SVL; head width 32.6 and 33.3% ($\bar{x} = 33.0$) of SVL; snout moderately short, bluntly rounded in dorsal view, rounded above and truncate in profile; loreal region flat; nostrils barely protuberant laterally, anterior edge at level of anterior border of lower jaw; eye–nostril distance 71.0 and 72.2% ($\bar{x} = 71.6$) length of eye; supratympanic bulge rather massive, diffuse, covering posterodorsal part of tympanum; length of tympanum 47.2–52.6% ($\bar{x} = 49.9$) length of eye, separated from eye by distance about one-tenth length of eye.

Forelimb long, moderately robust, Finger I longer than Finger II; fingers unwebbed, bearing lateral fringes; Finger III not swollen in males; terminal discs expanded, about half again width of penultimate phalanges; subarticular tubercles moderately large, subconical; supernumerary tubercles absent; palmar tubercle large, round, elevated; thenar tubercle small, ovoid; nuptial excrescences absent. Hind limb short, robust; tibia length 45.4–47.6% ($\bar{x} = 46.5$) SVL; foot length 44.7–46.5% ($\bar{x} = 45.6$) SVL; outer tarsal fold absent; inner tarsal fold low, shallow sigmoid curve on distal one-half of tarsus; inner metatarsal tubercle small, nearly round; outer metatarsal tubercle larger than inner, round, separated from inner tubercle by large, ovoid median metatarsal tubercle; toes about one-fourth webbed; webbing formula II—(2–2')II(2–2')—3III(3–3')—4IV4—2'V;



Fig. 11. *Colostethus mittermeieri*, KU 211944, male, 27.2 mm.

lateral fringes present on toes; terminal discs expanded, about half again width of penultimate phalanges; subarticular tubercles small, subconical; supernumerary tubercles absent.

Skin on dorsum of body and hind limbs finely shagreen with scattered, minute tubercles in supraclacal region; skin on flanks shagreen; skin of ventral surfaces smooth; cloacal opening directed posteriorly at upper level of thighs; cloacal sheath short, wrinkled. Tongue elongately cordiform, widest and barely indented posteriorly, free behind for about half its length; median lingual process absent.

Color in preservative: Dorsum of head and body dull brown with many small, irregular, faintly darker brown markings (Fig. 11); flanks dull brown, slightly darker than dorsum; dorsolateral stripe absent; oblique lateral stripe absent, but white dash (one side) or two elongate white spots (other side) in inguinal region of holotype and faint tan stripe in inguinal region in KU 211944; ventrolateral stripe absent; forelimbs pale brown; dorsal surfaces of hind limbs pale brown with barely discernible darker brown transverse marking; anterior surfaces of thighs pale brown; posterior surfaces of thighs brown with diffuse cream mottling; upper lip tan, continuous cross snout. Venter cream with brown spots anterolaterally on throat and diffuse brown pigment on throat, chest, and anterior part of abdomen; palmar and plantar surfaces tan; brownish gray transverse marks on dorsal and ventral surfaces digits.

Color in life: Unknown. Unfortunately, the single new specimen (KU 211944) was confused with individuals of *Colostethus aeruginosus* in the field and no color notes or photographs were taken.

Distribution and ecology.—This species is known from only two localities at elevations of 1620 and 2050 m in humid cloud forest on the eastern slope of the northern

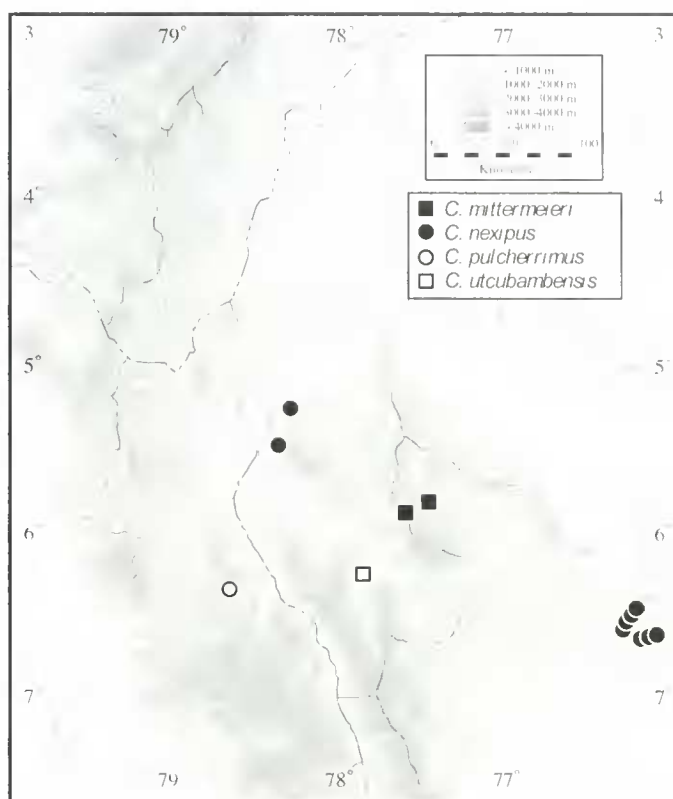


Fig. 12. Localities of occurrence of four species of *Colostethus*.

part of the Cordillera Central in Departamento San Martín, Peru (Fig. 12). Both localities are on the road from Balzapata to La Rioja. The specimen from 2050 m was in a small, mossy stream by day.

Remarks.—I compared KU 211944 with the holotype (MCZA-100217); the two specimens are extremely similar and differ only in KU 211944 having slightly less webbing and less tuberculate skin in the supraclacal region. However, there are several discrepancies between the holotype and its description by Rivero (1991a). Rivero stated that Finger I was shorter than Finger II (longer, and shown as longer in his Figure 1) and that lateral fringes were absent on the fingers (definitely present). Rivero (1991a) mentioned lateral white stripes on the lower flanks and black longitudinal streaks on the forelimbs; although I did not observe these, more than a decade has elapsed since Rivero examined the specimens, and some of the pattern may have been lost. However, I did not observe those features on KU 211944. Rivero (1991a:6) referred to the dorsum of the holotype as "solid dark grayish brown"; there are distinct, darker brown marks on the dorsum. Furthermore, Rivero (1991a:8) provided measurements and proportions of three "males." These specimens have been examined by Taran Grant, who stated that all three are juvenile females (Grant, in litt.).

Colostethus nexipus Frost

Colostethus nexipus Frost, 1986:214. Holotype: BMNH 1983.1061 from Los Tayos, Provincia de Morona-Santiago, Ecuador. Coloma, 1995:44.

Colostethus citreicola Ravero, 1991b:11. Holotype: USNM 282687 from the immediate vicinity of Limón (General Plaza), 1097 m, Provincia Morona-Santiago, Ecuador [Synonymy fide Coloma, 1995:44].

Diagnosis.—A large species of *Colostethus* with the following characteristics: (1) maximum SVL in males 30.0 mm, in females 33.0 mm; (2) disc on Finger III expanded, half again width of penultimate phalange; (3) Finger I shorter than Finger II; (4) lateral fringes present as narrow ridges on fingers; (5) disc on Toe IV expanded, half again width of penultimate phalange; (6) lateral fringes present on toes; (7) inner tarsal fold weak or absent; tarsal tubercle absent; (8) toes about half webbed; (9) dorsolateral stripe present; (10) oblique lateral stripe present; (11) ventrolateral stripe absent; (12) gular-chest region cream; (13) abdomen cream; (14) no sexual dimorphism in ventral coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes black.

Relatively few species of *Colostethus* Ecuador and Peru have Finger I shorter than Finger II; with the exception of *C. nexipus* and *C. patitae*, all of these species (*C. awa*, *chocoensis*, *fuliginosus*, *idiomelus*, *maquipucuna*, *peculiaris*, *pulchellus*, and *pumilus*) lack a dorsolateral stripe, which is prominent in *C. nexipus*. According to Lötters et al. (2003), *C. patitae* differs from *C. nexipus* by lacking webbing between

Relatively few species of *Colostethus* Ecuador and Peru have Finger I shorter than Finger II; with the exception of *C. nexipus* and *C. patitae*, all of these species (*C. awa*, *chocoensis*, *fuliginosus*, *idiomelus*, *maquipucuna*, *peculiaris*, *pulchellus*, and *pumilus*) lack a dorsolateral stripe, which is prominent in *C. nexipus*. According to Lötters et al. (2003), *C. patitae* differs from *C. nexipus* by lacking webbing between the toes and in having a bright yellow (instead of orange) dorsolateral stripe. Four other species have the toes at least half webbed; these are *C. fuliginosus*, *leucophaeus*, *peculiaris*, and *sordidatus*, all of which lack a dorsolateral stripe. Fingers I and II are equal in length in *C. sordidatus* and Finger I is longer than Finger II in *C. leucophaeus*. Four species (*C. bocagei*, *chocoensis*, *mittermeieri*, and *sauli*) are smaller (males < 25 mm, females < 30 mm) and have less extensive webbing than *C. nexipus*. Furthermore, all four species lack dorsolateral stripes; Fingers I and II are equal in length in *C. bocagei* and *C. sauli*, and Finger I is longer than Finger II in *C. mittermeieri*. The toes are only webbed basally in *C. awa*, *elachylistus*, *fugax*, *infraguttatus*, and *syleuticus*, all of which also differ from *C. nexipus* by

lacking dorsolateral stripes. The smaller *C. awa* also has less webbing and Finger I shorter than Finger II. All other *Colostethus* in the region either lack webbing or if basal webbing is present (usually only between Toes III and IV), they are smaller in size and have Finger I longer than Finger II; these include *C. alessandroi*, *brunneus*, *conspicuus*, *fratisenescus*, *fuscellus*, *gasconi*, *insperatus*, *machalilla*, *marchesianus*, *mediarmidi*, *melanolaeus*, *stephensi*, *toachi*, *trilineatus*, and *vanzolinius* (Coloma, 1995; Grant and Rodríguez, 2001; Morales, 2002).

Description.—Frost's (1986) original description that was supplemented by Coloma (1995) can be expanded considerably by the series of specimens from northern Peru ($N = 10$ males, 11 females, 5 juveniles). Body robust; SVL in males 18.6–20.5 ($\bar{x} = 19.3$) mm, in females 20.0–23.1 ($\bar{x} = 21.4$) mm; head about as long as wide; head length 31.2–38.1% ($\bar{x} = 35.6$) of SVL; head width 31.2–37.6% ($\bar{x} = 35.4$) of SVL; snout moderately short, bluntly rounded in dorsal view, bluntly rounded above and inclined posteroventrally in profile; loreal region flat; nostrils not protuberant laterally, with posterior border at level of anterior margin of lower jaw; eye-nostril distance 58.1–75.0% ($\bar{x} = 63.9$) of length of eye; supratympanic bulge diffuse, barely obscuring posterodorsal edge of tympanum; length of tympanum 40.7–46.9% ($\bar{x} = 44.2$) of length of eye, separated from eye by distance about one-fifth length of eye; tympanic annulus distinct.

Forelimb long, moderately slender; Finger I shorter than Finger II; fingers unwebbed, bearing narrow lateral fringes; Finger III not swollen in males; terminal discs expanded, about half again width of penultimate phalanges; subarticular tubercles small, rounded; supernumerary tubercles absent; palmar tubercle large, nearly ovoid; thenar tubercle slightly smaller, elliptical; nuptial excrescences absent. Hind limb short, moderately robust; tibia length 44.7–54.8% ($\bar{x} = 50.1$) of SVL; foot length 43.0–53.1% ($\bar{x} = 47.8$) of SVL; outer tarsal fold and tarsal tubercle absent; inner tarsal fold low, shallowly sigmoid on distal half of tarsus; inner metatarsal tubercle low, ovoid; outer metatarsal tubercle subconical; toes about half webbed; modal webbing formula I1–2III1–2III1–3IV3–IV; lateral fringes present distally to webbing; terminal discs expanded, about half again width of penultimate phalanges; subarticular tubercles small, rounded; supernumerary tubercles absent.

Skin on dorsum of body and hind limbs finely shagreen with minute tubercles postsacally on body; skin on flanks shagreen; skin of ventral surfaces smooth, except for weak granules on posterior part of abdomen; cloacal opening directed ventrally at midlevel of thighs; cloacal sheath short. Tongue long, widest and shallowly notched posteriorly, free behind for about two thirds of its length; median lingual process absent.

In a phylogenetic tree of some dendrobatid frogs based on molecular data, Santos et al. (2003) included *Colostethus bocagei* and *C. maculosus*. The latter is a junior subjective synonym of *C. bocagei* (Coloma, 1995). One of the authors of Santos et al. (Iris A. Coloma) informed me (in litt., 22 July 2004) that "Our recognition [of *C. maculosus*] was not justified."

Color in preservative: Dorsum of head, body, and limbs brown, with or without irregular dark brown mid-dorsal marks on body; tan dorsolateral stripe extending from posterior margin of upper eyelid to paracloacal region, becoming diffuse or fragmented postsacrally, bordered above and below by dark brown stripes; lower brown stripe continuation of facial stripe across snout and through eye and tympanum; creamy tan oblique lateral stripe extending from groin to point above insertion of upper, fragmented posteriorly in four individuals. Flanks below stripes brown; limbs brown with dark brown transverse bars, extending onto anterior and posterior surfaces of thighs; upper lip creamy tan. Ventral surfaces of body and limbs creamy tan; minute brown flecks on throat and chest in some specimens; palmar and plantar surfaces pale brown.

Color in life: Dorsum of head and body dull brown to nearly black, usually with darker brown or black irregular marks; flanks black; dorsolateral stripes originating on snout and extending to paracloacal area, curved slightly medially at midlength of body, variable in color from nearly red to most commonly orange or to tan; in some individuals, changing from orange anteriorly to bluish tan posteriorly; oblique lateral stripe cream, pale orange, or usually bluish white (Fig. 6C). Upper lip and proximal dorsal surface of upper arm creamy tan to pale yellow; dorsal surfaces of hind limbs tan to pale bluish gray with dark brown transverse bars or less commonly irregular marks; anterior and posterior surfaces of thighs and ventral surfaces of limbs bluish gray; digital scutes white to pale gray; throat and belly white to pale yellow; iris reddish copper.

Tadpoles.—A male having a SVL of 19.7 mm was transporting 12 tadpoles on 15 February 1989. The tadpoles have body lengths of 3.6–3.8 mm (\bar{x} = 3.66) and total lengths of 8.7–8.9 mm (\bar{x} = 8.80). These small tadpoles are in Stage 24; the oral disc and associated structures are not developed, and the body cavity is filled with yolk.

Free-swimming tadpoles were found in a pool in a stream and in a pool adjacent to another stream. Tadpoles are in various stages from Stage 25 to metamorphosis (Table 10); these tadpoles are associated with *Colostethus nexipus* by the toes being about half webbed in metamorphosing young and by the dorsolateral stripe in large individuals. Furthermore, *Colostethus nexipus* was the only member of the genus found at localities where the tadpoles were collected.

A typical tadpole (KU 215594) in Stage 37 has a body length of 9.2 mm and a total length of 30.5 mm; body ovoid, wider (5.4 mm) than high (3.5 mm); snout bluntly rounded in dorsal view, rounded in profile; nares directed anteriorly about midway between tip of snout and orbits; eyes large (1.3 mm), situated and directed dorsolaterally, not visible

Table 10. Measurements (in mm) of tree-swimming tadpoles of *Colostethus nexipus*. Range of variation followed by mean in parentheses.

Stage	N	Body length	Total length
25	2	5.3–6.2 (\bar{x} = 5.75)	12.7–15.8 (\bar{x} =
14.25)			
28	2	6.5	16.0
29	1	6.6	18.5
31	3	7.5–8.7 (\bar{x} = 8.00)	20.5–22.4 (\bar{x} =
21.17)			
32	2	7.9–8.5 (\bar{x} = 8.20)	19.1–23.3 (\bar{x} =
21.20)			
34	2	8.9–9.0 (\bar{x} = 8.95)	23.3
37	3	8.8–9.2 (\bar{x} = 8.97)	28.4–30.5 (\bar{x} =
29.3)			
39	1	9.8	24.5

from below; interorbital distance 1.7 mm; spiracle sinistral; tube short, attached to body for its entire length; spiracular opening directed posterodorsally well below midline at about two thirds of length of body; cloacal tube short, dextral, attached to ventral fin. Caudal musculature robust, about equal in height on proximal third of tail, gradually diminishing to pointed terminus; dorsal fin originating on base of caudal musculature, greatest height at midlength of tail, gradually diminishing to acutely rounded tip; ventral fin originating on body wall, about equal in height throughout its length; at midlength of tail, dorsal fin slightly higher than ventral fin and about equal to height of caudal musculature (Fig. 9F).

Oral disc 2 mm wide, directed anteroventrally; median two thirds of anterior labium bare; elsewhere, labia with single row of subconical marginal papillae; submarginal papillae absent; labia with shallow lateral folds bearing few small, rounded papillae. Jaw sheaths moderately slender, coarsely serrate; anterior sheath forming broad arch; posterior sheath broadly V-shaped; LTRF 2(1)/3; anterior rows slightly longer than posterior rows.

In preservative, dorsum and sides of body dark reddish brown with minute white flecks; caudal musculature tan, reddish brown dorsally; fins translucent, essentially unmarked (Fig. 9F); individuals in Stage 41 with larger, bluish-white lichenous flecks on all body surfaces. In life, body dark brown with tan dorsolateral stripe in largest individuals; tail tan with brown flecks.

Distribution and ecology.—This species is widely distributed in departamentos of Amazonas and San Martín in northern Peru, where it has been taken at an elevation of 360 m in the floodplain of the Río Huallaga, elevations up to 810 m in a spur of the Andes northeast of Tarapoto, and at an elevations of 325 and 520 m on the western slope

of the northern part of the Cordillera Central (Fig. 12). Most of these localities are at lower elevations than those in southern Ecuador, where the species has been found at elevations of 500–1500 m (Coloma, 1995). All Peruvian specimens were associated with rocky streams in February; most were active by day, but a few were on boulders in streams at night. One juvenile and one adult male carrying tadpoles were on leaves in the spray zone of a waterfall at night; another male carrying tadpoles was on a rock in a stream by day. Free-swimming tadpoles were in pools in streams.

At Ponga de Shilcayo, a narrow ravine at an elevation of 470 m, 4 km NNW of Tarapoto, *Colostethus nexipus* is sympatric with seven other dendrobatid frogs—*Colostethus ornatus*, *Cryptophyllobates azureiventris*, *Dendrobates fantasticus*, *D. imitator*, *Epipedobates bassleri*, *E. hahnelti*, and *E. trivittatus*. Only *C. nexipus* was found along the rocky stream in the ravine; the other dendrobatids were on moss-covered boulders, on the forest floor, or in terrestrial bromeliads (*D. fantasticus*).

Remarks.—*Colostethus nexipus* is one of the most brightly colored members of the genus; the presence of skin toxins in *C. nexipus* has not been determined. In the most extensive molecular phylogeny of dendrobatids (Santos et al., 2003), *C. nexipus* is the sister taxon of an aposematic species, *Cryptophyllobates azureiventris*.

Colostethus ornatus Morales

Colostethus ornatus Morales, 2002:37. Holotype: MHNSM 17713 from Tarapoto, 350 m, Provincia San Martín, Departamento de San Martín, Peru.

Diagnosis.—A small species of *Colostethus* with the following characteristics: (1) maximum SVL in males 16.9 mm, in females 18.4 mm; (2) disc on Finger III expanded, half again width of penultimate phalange; (3) Finger I longer than Finger II; (4) lateral fringes absent on fingers; (5) disc on Toe IV expanded, half again width of penultimate phalange; (6) lateral fringes absent on toes; (7) inner and outer tarsal folds absent; outer tarsal tubercle present; (8) basal webbing present between Toes II and IV; elsewhere webbing absent; (9) dorsolateral stripe present; (10) oblique lateral stripe absent; (11) ventrolateral stripe present; (12) gular-chest region gray in male, white in female; (13) abdomen creamy white; (14) sexual dimorphism in coloration; (15) median lingual process absent; (16) Finger III swollen in males; (17) color of testes unknown.

The only other species of *Colostethus* in Ecuador and Peru with Finger I longer than Finger II, dorsolateral and ventrolateral stripes, and no oblique lateral stripe is *C. talamancae*, a larger frog (SVL to 24 mm) that is confined to the Chocóan Region and that also differs from *C. ornatus* by having lateral fringes on the fingers and toes. Furthermore, the middorsum of *C. talamancae* is essentially uniform dark brown, whereas a rhomboidal dark brown

mark is present on the tan dorsum of *C. ornatus*, in which the posterior surfaces of the thighs lack the hook-shaped dark mark characteristic of *C. talamancae* (Savage, 1968).

Description.—The description of this species by Morales (2002) is minimally adequate. Here, it is augmented by a description of a paratype (adult female, KU 211950) from Ponga de Shilcayo, Departamento de San Martín.

Body slender; head longer than wide; head length 32.9% of SVL; head width 30.6% of SVL; snout long, broadly truncate in dorsal view, bluntly rounded in profile; loreal region flat; nares not protuberant, posterior margins at level of anterior margin of lower jaw; eye–nostril distance 58.3% of length of eye; supratympanic bulge diffuse, barely obscuring upper edge of tympanum; otherwise, tympanic annulus distinct; length of tympanum 50% of length of eye, separated from eye by about one-fourth length of eye.

Forelimb long, slender; Finger I much longer than Finger II; fingers not webbed, lacking lateral fringes; Finger III not swollen in males (fide Morales, 2002); terminal discs expanded, about half again width of penultimate phalanges; subarticular tubercles large, subconical; supernumerary tubercles absent; palmar tubercle large, nearly round; thenar tubercle large, elliptical. Hind limb moderately short, slender; tibia length 50.3% of SVL; foot length 46.8% of SVL; tarsal folds absent; inner tarsal tubercle small, elongate; inner metatarsal tubercle elliptical; outer metatarsal tubercle small, subconical; toes long, slender, with basal webbing between Toes II and III and between Toes III and IV; lateral fringes absent; terminal discs expanded, about half again width of penultimate phalanges; subarticular tubercles small, subconical; supernumerary tubercles absent.

Skin on all surfaces smooth; cloacal opening directed posteroventrally at upper level of thighs; cloacal sheath short. Tongue long, widest posteriorly, not notched posteriorly, free behind for about half of its length.

Color in preservative: Dorsum tan with brown markings consisting of a broad, diffuse interorbital bar, X-shaped mark in scapular region with anterior arms of X extending to eyelids and posterior arms confluent with diagonal marks connected to teardrop-shaped mark on posterior part of dorsum; broad, dark brown stripe across snout, through loreal and supratympanic regions, to groin, bordered above by tan dorsolateral stripe. Hind limbs tan with single, broad transverse bar each on thigh, shank, and foot; anterior surfaces of thighs tan; posterior surfaces brown; forelimbs cream with dark brown longitudinal stripe on posterior surface of upper arm; upper lip, lower half of tympanum, and lower part of flank cream; venter and palmar surfaces cream; plantar surfaces brown.

Color in life: Dorsum tan with brown markings, consisting of an interorbital bar, X-shaped mark in scapular region; posterior parts of X-shaped mark connected to a roughly triangular mark in sacral region; dorsolateral

stripe pale yellow, narrow on head, diffuse on body; broad, dark brown stripe across tip of snout, through loreal and tympanic regions becoming broader on flank and extending to groin, bordered below on flanks by narrow pale yellow ventrolateral stripe; oblique lateral stripe absent; flanks below stripe creamy tan with brown flecks; dorsal surfaces of hind limbs grayish brown with many small dark brown flecks and one broad transverse brown bar on thigh, shank, and foot; posterior surfaces of thighs brown; labial region creamy white with brown flecks; throat and belly pale lemon yellow; ventral surfaces of limbs flesh colored; digital scutes pale gray in contrast to adjacent dark brown surfaces; iris greenish bronze (Fig. 6D).

Measurements (in mm): SVL 17.3, tibia length 8.7, foot length 8.1, head width 5.3, head length 5.7, eye-nostril distance 1.4, length of eye, 2.4, length of tympanum 1.2.

Distribution and ecology.—This small species is known only from the vicinity of Tarapoto in northeastern Peru, where it has been found at elevations of 350–680 m in disturbed lowland rainforest and lower humid montane forest (Fig. 4). Morales (2002) provided no ecological data on the species; an individual was active on the forest floor by day in February.

Remarks.—Morales (2002) designated KU 211950 as a paratype of *Colostethus ornatus* from 12 km northeast of Tarapoto, 720 m, Departamento de San Martín, Peru. The locality given is erroneous; the specimen is from Ponga de Shilcayo, about 4 km NNW of Tarapoto, 470 m.

The color pattern of KU 211950 resembles that of the holotype illustrated by Morales (2002), except that the anterior part of the X-shaped mark on the head is separated from that part in the scapular region.

The single female examined contained six large, unpigmented ovarian eggs about 2 mm in diameter. The sizes of the ovarian complement and of the ovarian eggs are like those of *Colostethus stepheni* (Junc., 1998). The eggs of *C. stepheni* hatch into non-feeding nidicolous tadpoles that complete their development in the terrestrial nest (Junc. et al., 1994). Thus, *C. ornatus* may be another member of the genus with nidicolous tadpoles.

Colostethus poecilonotus Rivero

Colostethus poecilonotus Rivero, 1991a:13. Holotype: MCZ A-89108 from Alva, Departamento Amazonas, Peru.

Diagnosis.—A moderate-sized species of *Colostethus* with the following characteristics: (1) maximum SVL in males 19.7 mm, in females 25.2 mm; (2) disc on Finger III slightly expanded; (3) Finger I equal in length to Finger II; (4) lateral fringes absent on fingers; (5) disc on Toe IV slightly expanded; (6) lateral fringes absent on toes; (7) outer tarsal fold and tarsal tubercle absent; inner tarsal fold curved on distal half of tarsus; (8) toes unwebbed; (9) dorsolateral stripe absent; (10) oblique lateral stripe

present from groin to midflank; (11) ventrolateral stripe absent; (12) gular-chest region uniform creamy tan; (13) abdomen creamy tan; (14) no sexual dimorphism in ventral coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

Many species of *Colostethus* in the region lack a dorsolateral stripe and have an oblique lateral stripe and Fingers I and II equal in length. Of these, only *C. bocagei* has a short oblique lateral stripe; in the others (*C. anthracinus*, *breviquartus*, *cevallosi*, *delatorreae*, *elachylistus*, *fugax*, *idiomelus*, *infraguttatus*, *leimanni*, *sauli*, and *vertebralis*), the oblique lateral stripe extends anteriorly to, or nearly to, the eye, instead of only to the midflank as in *C. poecilonotus*. Of these species, *C. cevallosi* and *C. leimanni* also differ from *C. poecilonotus* by having black arm bands, as defined by Grant and Ardila-Robayo (2002). Furthermore, *C. elachylistus*, *fugax*, *sauli*, and *sordidatus* also differ from *C. poecilonotus* by having webbing between the toes, and *C. elachylistus*, *infraguttatus*, *idiomelus*, and *sauli* have lateral fringes on the fingers and toes. Other species with an oblique lateral stripe but no dorsolateral stripe (*C. idiomelus* and *C. insulatus*) have Finger I longer than Finger II, and in *C. insulatus*, the oblique lateral stripe extends anteriorly to the eye. The only other species in the region having Fingers I and II equal in length are *C. sylvaticus*, which has lateral fringes on the digits, a dorsolateral stripe, and no oblique lateral stripe, and *C. exasperatus*, which has dorsolateral and oblique lateral stripes, and lateral part of the abdomen marbled.

Description.—(N = 4: 1 male, 3 females). Body moderately robust; head slightly longer than wide; head length 32.9–36.5% (\bar{x} = 34.1) of SVL; head width 29.4–32.4% (\bar{x} = 30.8) of SVL; snout moderately long, bluntly rounded, nearly truncate in dorsal view, truncate in profile; loreal region flat; nostrils slightly protuberant laterally, with posterior border at level well behind anterior margin of lower jaw; eye-nostril distance 65.3–69.0% (\bar{x} = 67.0) length of eye; supratympanic bulge diffuse, covering posterodorsal part of tympanum; length of tympanum 51.7–60.0% (\bar{x} = 55.2) length of eye, separated from eye by distance about one-sixth length of eye; tympanic annulus evident externally only anteriorly and ventrally.

Forelimb long, moderately slender; Fingers I and II equal in length; fingers unwebbed, lacking lateral fringes; Finger III not swollen in males; terminal discs slightly expanded, barely wider than penultimate phalanges; subarticular tubercles large, rounded; supernumerary tubercles absent; palmar tubercle large, rounded; thenar tubercle small, elliptical; nuptial excrescences absent. Hind limb short, robust; tibia length 44.0–48.2% (\bar{x} = 46.2) SVL; foot length 42.8–50.8% (\bar{x} = 46.3) SVL; outer tarsal fold absent; inner tarsal fold shallowly sigmoid on distal half of tarsus; inner metatarsal tubercle small, elliptical; outer metatarsal

tubercle equal in size, subconical; toes unwebbed, lacking lateral fringes; terminal discs expanded barely expanded; subarticular tubercles small, round; supernumerary tubercles absent.

Skin on dorsum of body and hind limbs shagreen with small tubercles postsacrally and larger tubercles in tympanic region; skin on flanks shagreen; skin of posterior part of abdomen finely granular; other ventral surfaces smooth; cloacal opening directed posteroventrally at mid-level of thighs; cloacal sheath short. Tongue ovoid, widest posteriorly, not notched, free behind for about half of its length; median lingual process absent.

Color in preservative: Dorsum of head and body brown with many small, nearly round, dark brown spots; dark brown stripe across tip of snout extending through loreal and supratympanic regions, continuous with dark brown flanks with irregular creamy white spots ventrally; pale dorsolateral stripe absent; pale tan to dull white oblique lateral stripe extending from groin to point between axilla and midflank; ventrolateral stripe absent; upper lip and tympanic region tan with faint grayish brown irregular markings. Forelimb pale brown with dark brown transverse bars on forearm and dark brown longitudinal stripes on anterior and posterior surfaces of upper arm; dorsal surfaces of hind limbs brown with narrow dark brown transverse bars; anterior surface of thigh tan with longitudinal dark brown stripe; posterior surface of thigh brown with diffuse creamy white longitudinal stripe. All ventral surfaces creamy tan, except plantar surfaces brown.

Color in life: Unknown.

Distribution and ecology.—*Colostethus poecilonotus* is known only from the type locality at an elevation of 1000 m on the slopes of the Cordillera Central above the Rlo Utucubamba Valley, which is mostly cultivated but otherwise mainly supports thorn forest (Fig. 10).

Remarks.—Examination of the type series revealed several discrepancies between the specimens and Rivero's (1991a) description; he correctly stated that Fingers I and II are equal in length, but his illustration (Fig. 5) clearly shows the first finger much longer than the second. Rivero (1991a) reported all four specimens to be adult females; dissection revealed that one of the paratypes (MCZ A-89109) to be an adult male. Measurements and proportions reported here differ slightly from those given by Rivero.

Colostethus pulcherrimus new species

Holotype.—KU 211946, an adult female, from the immediate vicinity of Cutervo (06° 22' S, 78° 49' W, 2620 m), Provincia de Cutervo, Departamento de Cajamarca, Peru;

one of a series collected by Fernando M. Cuadros and John J. Wiens on 26 February 1989.

Paratypes.—KU 211947–49 and MHNSM 6251 collected with the holotype.

Diagnosis.—A moderately large species of *Colostethus* with the following characteristics: (1) maximum SVL in males 28.2 mm, in females 29.7 mm; (2) disc on Finger III expanded, slightly wider than penultimate phalange; (3) Finger I longer than Finger II; (4) lateral fringes present on fingers; (5) disc on Toes IV expanded, slightly wider than penultimate phalange; (6) lateral fringes present on toes; (7) outer tarsal fold and tarsal tubercle absent; inner tarsal fold curved on distal half of tarsus; (8) webbing absent between toes; (9) dorsolateral stripe absent; (10) oblique lateral stripe present; (11) ventrolateral stripe absent; (12) gular-chest area cream with or without brown mottling; (13) abdomen cream with or without brown mottling; (14) no sexual dimorphism in ventral coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

Of the other species in Ecuador and northern Peru that have the Finger I longer than Finger II, an oblique lateral stripe, and no dorsolateral stripe, *Colostethus argyrogaster* differs from *C. pulcherrimus* by having a pale ventrolateral stripe, orange inguinal region in life, no fringes on the digits, and basal webbing only between the Toes III and IV. *Colostethus leucophaeus* differs by having the toes about half webbed. *Colostethus fugax* and *C. machalilla* differ by having the Finger III swollen in males and by lacking fringes on the digits. The equally large *C. toachi* also lacks fringes on the digits and has a pale ventrolateral stripe, as does *C. melanolaemus*, in which the oblique lateral stripe is diffuse.

Description.—($N = 5$: 1 male, 4 females). Body robust; head slightly longer than wide; head length 30.9–33.7% ($\bar{x} = 33.1$) of SVL; head width 29.1–31.8% ($\bar{x} = 29.9$) of SVL; snout short, rounded in dorsal view, bluntly rounded in profile; loreal region flat; nostrils not protuberant, anterior border at level slightly posterior to anterior margin of lower jaw; eye–nostril distance 62.5–70.0% ($\bar{x} = 66.9$) of length of eye; supratympanic bulge diffuse, covering upper and posterodorsal edges of tympanum; tympanic annulus distinct; length of tympanum 59.4–66.7% ($\bar{x} = 63.7$) of length of eye, separated from eye by distance about one-fourth length of tympanum.

Forelimb moderately short, robust; Finger I longer than Finger II; fingers unwebbed, bearing narrow lateral fringes; Finger III not swollen in males; terminal discs expanded, slightly wider than penultimate phalanges; subarticular tubercles low, rounded; supernumerary tubercles absent;

palmar tubercle large, nearly round; thenar tubercle large, elliptical; nuptial excrescences absent. Hind limb short, robust; tibia length 44.2–47.0% (\bar{x} = 45.2) of SVL; foot length 48.9–51.1% (\bar{x} = 49.9) of SVL; outer tarsal fold and tarsal tubercle absent; inner tarsal fold flaplike, forming sigmoid curve on distal half of tarsus; inner metatarsal tubercle small, elliptical; outer metatarsal tubercle small, subconical; toes unwebbed, bearing narrow lateral fringes; terminal discs expanded, slightly wider than penultimate phalanges; subarticular tubercles small, rounded; supernumerary tubercles absent.

Skin on dorsum of head, body, and hind limbs, and on venter smooth; skin on flanks finely shagreen; cloacal opening directed posteroventrally at upper level of thighs; cloacal sheath short. Tongue long, widest and shallowly notched posteriorly, free behind for about half of its length; median lingual process absent.

Color in preservative: Dorsum of head and body dull brown with faint, darker brown, irregular marks; flanks dark brown with cream flecks; upper lip tan with brown flecks; dorsolateral and ventrolateral stripes absent; oblique lateral stripe narrow, cream, extending from groin to posterior edge of orbit or midflank. Forelimbs brown; dorsal surfaces of hind limbs dull brown with darker brown transverse bars—three each on thigh, shank, and foot; anterior and posterior surfaces of thighs brown with cream mottling. Throat, chest, abdomen, and ventral surfaces of limbs cream with varying amounts of brown mottling—extensive in holotype, slight in one male and two females, negligible in one female; palmar and plantar surfaces brown.

Color in life: Dorsum of head and body pale grayish green with irregular coppery-brown irregular markings; oblique lateral stripe dull tan anteriorly, bluish white posteriorly; flanks black with blush-white flecks and streaks; upper lip pinkish tan, becoming white posteriorly; digital scutes pale gray bordered by black; iris bronze-brown (Fig. 6E).

Measurements of holotype (in mm): SVL 28.0, tibia length 12.6, foot length 14.3, head width 8.2, head length 8.8, eye-nostril distance 2.1, length of eye 3.2, length of tympanum 1.9.

Distribution and ecology.—This species is known only from two small streams in the immediate vicinity of Cuervo, a village at an elevation of 2620 m in a cultivated valley in the northern part of the Cordillera Occidental (Fig. 12). The frogs were active in the streams by day; adult *Colostethus elachylistus* were found in the same streams.

Etymology.—The specific name is a Latin adjective meaning “prettiest,” in reference to the rather striking coloration in contrast to the rather drab appearance of many species of *Colostethus* in the Peruvian Andes.

Colostethus sordidatus new species

Holotype.—KU 211960, adult female, from 30 km SW of Zapatero (about 10 km NE San José de Sisa [ca. 06°45' S, 76°33' W]), 500 m, Provincia de Lamas, Departamento de San Martín, Peru; one of a series collected by William E. Duellman and Rainer Schulte on 13 February 1989.

Paratopotypes.—KU 211961–72; same collectors and date.

Diagnosis.—A relatively large species of *Colostethus* with the following characteristics: (1) maximum SVL in males 29.9 mm, in females 36.1 mm; (2) disc on Finger III expanded, about twice width of penultimate phalange, nearly truncate; (3) Finger I equal in length to Finger II; (4) lateral fringes present on fingers; (5) disc on Toe IV expanded, about twice width of penultimate phalange; (6) lateral fringes present on toes; (7) outer tarsal fold and tarsal tubercle absent; inner tarsal fold curved on distal two-thirds of tarsus; (8) toes about two-thirds webbed; (9) dorsolateral stripe absent; (10) oblique lateral stripe present from groin to midflank; (11) ventrolateral stripe absent; (12) gular-chest region pale gray with dark gray intrusion laterally on throat; (13) abdomen creamy tan; (14) sexual dimorphism in ventral coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testes white.

Colostethus sordidatus is compared only with species that have webbing between the toes from Ecuador, Peru, Bolivia, and western Brazil. Three other species have the toes at least half webbed; these are *C. fuliginosus*, *nexipus*, and *peculiaris*. Both *C. nexipus* and *C. peculiaris* differ from *C. sordidatus* by having Finger I shorter than Finger II (equal in length in *C. sordidatus*); *C. nexipus* also differs by having a distinct pale dorsolateral stripe, whereas *C. peculiaris* also differs by lacking a pale oblique lateral stripe. Four species (*C. bocagei*, *chocoensis*, *mittermeieri*, and *sauli*) are smaller (males < 25 mm, females < 30 mm) and have less extensive webbing than *C. sordidatus*. Furthermore, in *C. chocoensis* Finger I is shorter than Finger II, whereas the opposite is the case in *C. mittermeieri*; Fingers I and II are equal in length in *C. bocagei*, *sauli*, and *sordidatus*. The only other species with moderately webbed toes, no dorsolateral and ventral stripes, and Fingers I and II equal in length are *C. elachylistus* and *C. infraguttatus*; in both of these species, the oblique lateral stripe extends anteriorly to the orbit (only to midflank in *C. sordidatus*). The smaller *C. atea* also has less webbing and Finger I shorter than Finger II. All other *Colostethus* in the region either lack webbing or if basal webbing is present (usually only between Toes

⁴Topotypic *Colostethus marchesianus* were described by Caldwell et al. (2002), who noted that most references to this species in Colombia, Ecuador and Peru applied to other species, many of which were named by Morales (2002).

III and IV, but also between Toes II and III at least in *C. marchesianus*⁴), they are smaller in size and have Finger I longer than Finger II; these include *C. alessandroi*, *brunneus*, *conspicuus*, *fratisenescus*, *fuscellus*, *gasconi*, *insperatus*, *machalilla*, *marchesianus*, *mediarmidi*, *melanolaemus*, *stepheni*, *toachi*, *trilineatus*, and *vanzolinius* (Coloma, 1995; Grant and Rodriguez, 2001; Morales, 2002).

Description.—(N = 11 ♂ males, 3 females). Body robust; head about as long as wide; head length 32.1–40.0% (\bar{x} = 36.2) of SVL; head width 31.9–38.8% (\bar{x} = 36.2) of SVL; snout moderately long, bluntly rounded in dorsal view, nearly truncate with slight posterolateral inclination in profile; loreal region flat; nostrils slightly protuberant laterally, with posterior border at level of anterior margin of lower jaw; eye-nostril distance 67.6–75.6% (\bar{x} = 71.4) length of eye; supratympanic bulge diffuse, covering upper edge of tympanum; length of tympanum 41.9–55.9% (\bar{x} = 49.3) length of eye, separated from eye by distance about one-fourth length of eye; tympanic annulus evident externally only anteriorly and ventrally.

Forelimb moderately long, robust; Fingers I and II equal in length; fingers unwebbed, bearing narrow lateral fringes; Finger III not swollen in males; terminal discs expanded, about twice width of penultimate phalanges; subarticular tubercles large, rounded; supernumerary tubercles absent; palmar tubercle large, broadly ovoid; thenar tubercle small, narrowly elliptical; nuptial excrescences absent. Hind limb short, robust; tibia length 42.9–50.4% (\bar{x} = 47.5) SVL; foot length 43.4–49.6% (\bar{x} = 46.3) SVL; outer tarsal fold absent; inner tarsal fold shallowly sigmoid on distal two-thirds of tarsus; inner metatarsal tubercle low, elongately elliptical; outer metatarsal tubercle round; toes about two-thirds webbed; modal webbing formula II–2III–2III–3IV–1V; lateral fringes present distally to webbing; terminal discs expanded, about twice width of penultimate phalanges; subarticular tubercles small, subconical; supernumerary tubercles absent.

Skin on dorsum of body and hind limbs finely shagreen; skin on flanks finely granular; skin of ventral surfaces smooth; cloacal opening directed posteroventrally at upper level of thighs; cloacal sheath short. Tongue about three times as long as wide, widest and shallowly notched posteriorly; free behind for about one-third of its length; median lingual process absent.

Color in preservative: Dorsum of head and body dull brown with scattered small brown spots; small, irregular white spots present on two males and two females; flanks dark brown; loreal and supratympanic stripe dark brown; pale dorsolateral and ventrolateral stripes absent; oblique lateral stripe dull white extending from groin to midflank; dorsal surfaces of upper arms and hind limbs brown with faint to distinct transverse darker brown bands—two on forearm and three each on thigh, shank, and foot; width

of transverse bars about equal to width of pale brown interspaces; anterior and posterior surfaces of brown with small, pale cream spots on the latter; margin of upper lip tan. Venter creamy tan with grayish-tan suffusion posterolaterally on throat and margin of lower jaw; anterior part of chin gray in one male; throat and chest gray in two males; palmar and plantar surfaces grayish brown; webbing translucent.

Color in life: Dorsum pale brown with irregular dark brown spots and transverse bars on limbs; posterior surfaces of thighs tan. Dark brown stripe across tip of snout, through nostril, to eye and continuous across tympanum, above insertion of forelimb, onto flank to groin; pale dorsolateral and ventrolateral stripes absent; dull white oblique lateral stripe extending from midflank to groin; dark brown crescent-shaped mark on anterior surface of upper arm not continuous with dark brown stripe on body; digital scutes grayish tan; upper lip pale creamy tan (Fig. 6G). Venter in males gray; venter in females white, with throat and chest bright yellow; white extending into axillary region (Fig. 6H). Iris reddish bronze with small black flecks and median horizontal brown streak.

Measurements of holotype (in mm): SVL 33.0; tibia length 15.5; foot length 14.5; head width 11.2; head length 11.7; eye-nostril distance 3.0; length of eye 4.3; length of tympanum 1.8.

Tadpoles.—Two kinds of *Colostethus* tadpoles were found at the type locality of *C. craspedocephus* and *C. sordidatus*. One kind resembles back-riding tadpoles associated with *C. craspedocephus*. The other presumably is *C. sordidatus* and is described below. Tadpoles were in a pool in a stream in a rocky ravine on 13 February 1989. One individual in Stage 34 has a body length of 16.2 mm and a total length of 42+ mm (tail incomplete). Eleven individuals in Stage 25 have body lengths of 8.1–13.1 mm (\bar{x} = 10.87) and total lengths of 19.4–33.5 mm (\bar{x} = 26.44).

A typical tadpole (KU 215611) in Stage 25 has a body length of 12.5 mm and a total length of 30.0; body globular, wider (8.8 mm) than height (6.7 mm); snout bluntly rounded in dorsal view, rounded in profile; nares directed dorsolaterally about midway between tip of snout and orbits; eyes small (1.2 mm), situated dorsally, directed dorsolaterally, not visible from below; interorbital distance 3.1 mm; spiracle sinistral, spiracular tube short, attached to body throughout its length; spiracular opening directed nearly posteriorly just below midline at about midlength of body; cloacal tube short, cone-shaped, dextral, attached to ventral fin. Caudal musculature robust, about equal height throughout proximal two-fifths of tail, gradually diminishing to pointed tip; dorsal fin originating on proximal part of caudal musculature, reaching greatest height at about two-thirds length of tail, declining to acutely rounded tip; ventral fin originating on body, highest at midlength; dor-

sal fin higher than ventral fin and both higher than caudal musculature at midlength of tail (Fig. 9G).

Oral disc 3.1 mm wide, directed anteroventrally; median half of anterior labium bare; elsewhere, labia bearing single row of small, subconical marginal papillae; labia with lateral folds with small, rounded papillae; submarginal papillae absent. Jaw sheaths narrow, finely serrate; anterior sheath forming broad arch; posterior sheath broadly V-shaped; LTRF 2(1)/3; A_2 longest, P_1 shortest.

In life, body brown; tail pale orange. In preservative, dorsum and sides of body brown; belly translucent; caudal musculature tan proximally, gray distally; fins translucent; scattered guanophores on body, caudal musculature and fins (Fig. 9G).

Distribution and Ecology.—This species is known only from the type locality at an elevation of 500 m near the eastern base of the Cordillera Central and from an elevation of 520 m southwest of Chiriaco near the northern end of the Cordillera Central (Fig. 4). At the type locality, individuals were under rocks in a streambed by day; at night, they were perched on wet boulders in the streambed. The call is a series of about 10 whistle-like notes.

Etymology.—The specific name, *sordidatus*, is Latin meaning “dressed shabbily” and refers to the drab dorsal coloration of this species.

Remarks.—The specimens from 20 km SW of Chiriaco (KU 196718–26) were collected on 17 and 18 December 1974 by Richard Thomas. This series contains two subadult females with SVLs of 21.3 and 26.5 mm and seven juveniles, two of which (SVLs of 10.3 and 12.0 mm) seem to be recent metamorphs. One of the subadult females has a few white spots on the dorsum.

Colostethus spilotogaster new species

Holotype.—LSUMNS 39341, adult female, from the west slope of the Cordillera Col-n, SE of La Peca, 8500 ft (= 2326 m) (ca. 05_37' S, 78_21' W), Provincia de Utcubamba, Departamento de Amazonas, Peru; obtained on 17 October 1978 by Thomas S. Schulenberg.

Diagnosis.—A moderate-sized species of *Colostethus* with the following characteristics: (1) SVL of males unknown; maximum SVL in female 24.0 mm; (2) disc on Finger III expanded, half again width of penultimate phalange; (3) Fingers I and II equal in length; (4) lateral fringes present on fingers; (5) disc on Toe IV expanded, half again width of penultimate phalange; (6) lateral fringes present on toes; (7) outer tarsal fold absent; tarsal tubercle present; inner tarsal fold slightly curved on distal half of tarsus; (8) webbing basal between toes; (9) dorsolateral stripe present; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) gular-chest region cream with brown spots; (13) abdomen cream with brown spots; (14) sexual

dimorphism in ventral coloration not known; (15) median lingual process absent; (16) nature of Finger III in males unknown; (17) color of testes unknown.

Six other species (*Colostethus*, *cleutherodactylus*, *exasperatus*, *nexipus*, *ornatus*, *sylvaticus*, and *utcubambensis*) in the region have pale dorsolateral stripes, but none has many small brown spots on the throat, chest, and abdomen as does *C. spilotogaster*. Four of those species (*C. cleutherodactylus*, *exasperatus*, *nexipus*, and *utcubambensis*) also differ from *C. spilotogaster* by having oblique lateral stripes. *Colostethus ornatus* also differs from *C. spilotogaster* by having a ventrolateral stripe and Finger I longer than Finger II; *C. sylvaticus* also differs by having a pair of large brown spots on the throat.

Description.—($N = 1$ female). Body moderately robust; head longer than wide; head length 37.1% of SVL; head width 34.2% of SVL; snout moderately short, broad, nearly truncate in dorsal view, truncate in profile; loreal region slightly concave; nostrils distinctly protuberant laterally, anterior border at level slightly posterior to anterior margin of lower jaw; eye–nostril distance 50% of length of eye; supratympanic bulge weak, obscuring posterodorsal edge of tympanum; tympanic annulus distinct, elevated; length of tympanum 78% of length of eye, separated from eye by distance about one-fifth length of eye.

Forelimb moderately long, slender; Fingers I and II equal in length; fingers unwebbed, bearing narrow lateral fringes; terminal discs expanded, width about half again width of penultimate phalanges; subarticular tubercles rounded; supernumerary tubercles absent; palmar tubercle large, round; thenar tubercle small, elliptical. Hind limb short, robust; tibia length 44.2% of SVL; foot length 41.2% of SVL; outer tarsal fold absent; inner tarsal fold originating at small tarsal tubercle, slightly curved on distal half of tarsus; inner metatarsal tubercle small, elliptical; outer metatarsal tubercle small, subconical; toes webbed basally, bearing narrow lateral fringes; terminal discs expanded, width about half again width of penultimate phalanges.

Skin on dorsum of head, body, and hind limbs smooth with scattered tubercles posteriorly on dorsum; skin on flanks finely granular; ventral surfaces smooth; cloacal opening directed posteroventrally at upper level of thighs; cloacal sheath short. Tongue long, widest and shallowly notched posteriorly, free behind for about one-half of its length; median lingual process absent.

Color in preservative: Dorsum of head and body dull brown with discontinuous middorsal longitudinal dark brown stripe; upper lip cream; flanks brown with cream tips on granules; upper lip cream; dorsolateral stripe pale tan, originating on snout, passing along canthus rostralis and outer edge of upper eyelid to upper insertion of hind limb, bordered below on head by broad dark brown stripe, bordered above on body by narrow dark brown stripe.



Fig. 13. *Colostethus spilotogaster*, USMNS 39341, female, 24.0 mm SVL.

Dorsal surfaces of hind limbs tan with indistinct brown spots; anterior and posterior surfaces of thighs brown with irregular small cream marks; forelimbs tan with dark brown longitudinal stripe on proximal part of anterior surface of upper arm and on entire length of posterior surfaces of upper arm. Venter cream with many small brown spots on throat, chest, and abdomen (Fig 13); palmar and plantar surfaces dark brown.

Color in life: Unknown.

Measurements of holotype (in mm): SVL 24.0, tibia length 10.6, foot length 10.0, head width 8.2, head length 8.9, eye-nostril distance 1.6, length of eye 3.2, length of tympanum 2.5.

Distribution and ecology.—This species is known only from the type locality at an elevation of 2326 m in humid montane forest on the western slopes of the Cordillera Col-n (Fig. 10). The only field notes accompanying the holotype are “leaf litter, cloud forest.”

Etymology.—The specific name is derived from the Greek *spilotos*, meaning spotted, and the Greek *gaster*, meaning belly; the name refers to the spotted venter in this species.

Remarks.—The distinctive combination of a spotted venter, dorsolateral stripe, and large tympanum sets *Colostethus spilotogaster* apart from all other species in the Andes of Ecuador and Peru; thus, the recognition of the species based on a single specimen is warranted.

The ornithological expedition by the Museum of Zoology at Louisiana State University in 1978 revealed the existence of an apparently endemic suite of anurans. In addition to the *Colostethus* named here, the endemics include *Gastrotheca abdita* (Duellman, 1987), *Eleutherodactylus atrabrachius*, *E. avicuporum*, and *E. cuneirostris* (Duellman

and Pramuk, 1999), and *Telmatobius colanensis* (Wiens, 1993).

Colostethus sylvaticus Barbour and Noble

Phylllobates sylvatica Barbour and Noble, 1920:396. Holotype: MCZ 5344 from Tabacónas (near Huancabamba), Departamento de Cajamarca, Peru.

Colostethus sylvatica—Edwards, 1971:148.

Diagnosis.—A relatively large species of *Colostethus* with the following characteristics: (1) maximum SVL in males 25.7 mm, in females 30.0 mm; (2) disc on Finger III slightly wider than penultimate phalange; (3) Finger I equal in length to Finger II; (4) lateral fringes present on fingers; (5) disc on Toe IV barely wider than penultimate phalange; (6) lateral fringes present on toes; (7) inner tarsal fold usually present; (8) toes unwebbed; (9) dorsolateral stripe present; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) gular-chest region pale with or without pair of dark spots on throat; (13) abdomen creamy white; (14) usually sexual dimorphism in ventral coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) Testis white.

Colostethus sylvaticus can be distinguished from most other species in the region by having the combination of Fingers I and II equal in length; dorsolateral stripe present, and oblique lateral stripe absent. *Colostethus idiomelus* shares this combination of characters, but it differs from *C. sylvaticus* by having narrower fringes on the fingers and toes, fewer transverse brown marks on the hind limbs (2 each on thigh and shank, instead of 3 or 4 as in *C. sylvaticus*), a narrower and less distinct dorsolateral stripe, and a mottled black and white throat (instead of yellow as in *C. sylvaticus*). Some individuals of *C. exasperatus* have the first and second fingers equal in length, but they have a short oblique lateral stripe (Coloma, 1995). *Colostethus eleutherodactylus* has Fingers I and II equal in length, but it differs from *C. sylvaticus* by having an oblique lateral stripe and greatly expanded discs on the digits. Likewise, *C. sordidatus* has Fingers I and II equal in length, but it differs from *C. sylvaticus* by having greatly expanded digits, an oblique lateral stripe, and no dorsolateral stripe.

Description.—(N = 21: 8 males, 13 females). Body robust; SVL 20.8–25.7 mm (\bar{x} = 23.8) in males, 27.1–30.0 mm (\bar{x} = 28.5) in females; head longer than wide; head length 39.9–36.5% (\bar{x} = 33.8) of SVL; head width 39.8–33.7% (\bar{x} = 32.1) of SVL; snout moderately long, bluntly rounded in dorsal view and in profile; loreal region flat; nostrils not protuberant, anterior border slightly posterior to level of anterior margin of lower jaw; eye-nostril distance 62.5–77.4% (\bar{x} = 68.6) length of eye; supratympanic bulge moderately massive, covering posterodorsal half of tympanum; length of tympanum 51.4–66.7% (\bar{x} = 59.5) length of eye, separated from eye by distance about one-fifth length of eye.

Forelimb moderately long, slender; Fingers I and II equal in length; fingers unwebbed, with narrow lateral fringes; Finger III not swollen in males; terminal discs slightly wider than penultimate phalanges; subarticular tubercles low, subconical; supernumerary tubercles absent; palmar tubercle large, round; thenar tubercle small, broadly ovoid; nuptial excrecences absent. Hind limb short, robust; tibia shorter than foot; tibia length 41.7–45.7% (\bar{x} = 43.9) SVL; foot length 45.7–52.3% (\bar{x} = 48.2) SVL; outer tarsal fold absent; inner tarsal fold, if evident, low, curved on distal half of tarsus; inner metatarsal tubercle elliptical; outer metatarsal tubercle subconical; toes unwebbed or with basal webbing between Toes IV and V, bearing narrow lateral fringes; terminal discs barely wider than penultimate phalanges; subarticular tubercles low, round, inconspicuous; supernumerary tubercles absent.

Skin on dorsum of body and hind limbs weakly shagreen; skin on flanks shagreen; skin of ventral surfaces smooth; cloacal opening directed posteroventrally at mid-level of thighs; cloacal sheath short. Tongue long, widest and notched posteriorly, free behind for about half of its length; median lingual process absent.

Color in preservative. Dorsum of head and body and flanks dull brown with irregular, darker brown markings ranging from flecks to dashes and chevrons; dark brown stripe in loreal and tympanic regions; upper lip dull brown; dorsolateral stripe dull tan, narrow on snout and edges of upper eyelids, broad and usually distinct on body, extending to groin, continuing as narrow stripe along upper insertion of hind limb and as diffuse stripe on anterior surface of thigh; oblique lateral stripe and ventrolateral stripe absent; arms pale brown with dark brown flecks; dorsal surfaces of hind limbs brown with dark brown transverse bars; anterior surfaces of thighs brown; posterior surfaces of thighs brown with cream flecks. Venter, including palmar and plantar surfaces pale tan; dusky suffusion on throat and chest forming diffuse paired brown spots posterolaterally on throat in some males.

Color in life: Dorsum olive-brown to coppery brown with dark brown to black flecks; digital scutes pale gray, contrasting to adjacent dark grayish-brown surfaces; upper lip and dorsolateral stripe creamy tan to pale bronze; throat, posterior part of belly and ventral surfaces of hind limbs dark yellow to orange; chest and anterior part of belly gray with black flecks; iris dull bronze with black flecks (Fig. 6F).

Tadpoles.— In February 1979, a male (KU 181673) having a SVL of 25.7 mm was transporting 15 tadpoles (KU 181868) 4.2–4.9 mm (\bar{x} = 4.50, N = 9) in body length and 12.1–13.2 mm (\bar{x} = 12.78, N = 9) in total length. In the same month, free-swimming tadpoles (KU 181869–70) were found in muddy pools at elevations of 2560 and 3010 m

Table 11. Measurements (in mm) of free-swimming tadpoles of *Colosteus sylvaticus*. Range of variation followed by mean in parentheses.

Stage	N	Body length	Total length
30	13	7.0–8.1 (\bar{x} = 7.42)	16.8–18.1 (\bar{x} = 17.46)
31	8	6.9–11.0 (\bar{x} = 8.32)	16.4–25.9 (\bar{x} = 19.42)
32	1	11.3	25.1
33	10	12.0–13.0 (\bar{x} = 12.47)	27.8–32.8 (\bar{x} = 29.05)
34	4	12.5–14.1 (\bar{x} = 13.27)	31.2–32.5 (\bar{x} = 31.80)
35	2	12.9–14.7 (\bar{x} = 13.80)	38.1–39.3 (\bar{x} = 38.50)

on the eastern slope of the Cordillera de Huancabamba, Departamento de Piura, Peru. The description of these tadpoles by Duellman and Wild (1993) is expanded herein (Table 11).

A typical tadpole (KU 181869) in Stage 33 has a body length of 13.0 mm and a total length of 29.4 mm; body ovoid, wider (7.2 mm) than high (5.5 mm); snout depressed, acutely rounded in dorsal view, rounded in profile; nares directed anterolaterally about midway between tip of snout and orbits; eyes small (1.1 mm), situated dorsally, directed dorsolaterally, not visible from below; interorbital distance 1.7 mm; spiracle sinistral; tube short, attached to body wall; spiracular opening directed posteriorly well below midline at about two-fifths length of body; cloacal tube short, dextral, attached to ventral fin. Caudal musculature moderately robust, about equal in height throughout proximal half of tail, then diminishing gradually to pointed terminus short of tip of tail; dorsal fin originating on proximal base of caudal musculature, highest at about two-thirds length of tail, diminishing to bluntly rounded tip; ventral fin originating on body wall, highest at midlength of tail, where each fin is slightly higher than caudal musculature (Fig. 9H).

Oral disc 3.0 mm wide, directed anteroventrally; median half of upper labium bare; elsewhere, labia bear single row of moderately large subconical marginal papillae; submarginal papillae absent; some individuals with two rows laterally; shallow lateral fold. Jaw sheaths moderately robust, finely serrate; anterior sheath in form of broad arch; posterior sheath widely V-shaped; LTRF 2/3(1); anterior rows slightly longer than posterior rows; P_3 shortest.

In preservative, dorsum of anterior part of body tan with dark brown interorbital blotch; posterior half of body dark brown; unpigmented transverse bands ventrally in some specimens; anterior part of venter transparent; caudal musculature pale tan with brown streak medially on each side of anterior fourth of tail; caudal fins translucent (Fig. 9H). In life, body and tail olive-tan with green lichenous markings dorsally on caudal musculature; belly greenish white; edge of oral disc yellow; iris pale bronze.

Distribution and ecology.—*Colostethus sylvaticus* is known from elevations of 2460–3100 m in the Cordillera de Cuchall, Cordillera de Huancabamba, and Cordillera de Tabaconas in northern Peru (Fig. 8). On the west slope of the Cordillera de Huancabamba, the species descends to 1920 m; its distribution there overlaps that of *C. elachyistus* at elevations of 1920–2590 m. These frogs have been found under rocks in, and along, streams and active along the streams in cloud forest by day. The call is a short trill.

Colostethus utubambensis Morales

Colostethus utubambensis Morales, 1994:103. Holotype: MHNSM 13986 from near Tingo (approximately 06°21' S, 77°49' W, 2391 m; but see remarks), Provincia de Luya, Departamento Amazonas, Peru.

Diagnosis.—A moderate-sized species of *Colostethus* with the following characteristics: (1) maximum SVL in males 19.8 mm, in females 26 mm; (2) disc on Finger III slightly expanded; (3) Finger I equal in length to, or longer than, Finger II; (4) lateral fringes absent on fingers; (5) disc on Toe IV slightly expanded; (6) lateral fringes absent on toes; (7) inner tarsal fold weak; (8) toes unwebbed; (9) dorsolateral stripe present; (10) oblique lateral stripe present; (11) ventrolateral stripe absent; (12) gular-chest area pale gray; (13) abdomen white or gray with diffuse white spots; (14) sexual dimorphism in ventral coloration; (15) median lingual process absent; (16) Finger III not swollen in males; (17) testis white.

Only three other species of *Colostethus* in Ecuador and northern Peru have dorsolateral and oblique lateral stripes; *C. nexipus* differs from *C. utubambensis* by having Finger I shorter than Finger II and by having lateral fringes on the digits and toes about half webbed. *Colostethus cleutherodactylus* differs by having Fingers I and II equal in length, greatly expanded terminal discs on the digits, and a well-developed, curved inner tarsal fold. *Colostethus kingsburyi* is like *C. utubambensis* in having Finger I longer than Finger II, but it differs by having a ventrolateral stripe.

Description.—(N = 3: 2 males, 1 female). Body moderately stout; head slightly longer than wide; head length 32.4–35.2% (\bar{x} = 33.9) of SVL; head width 29.2–31.2% (\bar{x} = 30.9) of SVL; snout truncate in dorsal view, slightly inclined posteroventrally in profile; loreal region flat; nostrils slightly protuberant laterally, with posterior edge at level of anterior margin of lower jaw; eye-nostril distance 66.7–75.0% (\bar{x} = 70.9) length of eye; supratympanic bulge diffuse, covering dorsal part of tympanum; length of tympanum 41.9–53.1% (\bar{x} = 46.5) length of eye, separated from eye by distance about one-fourth length of eye; tympanic annulus evident externally only anteriorly and ventrally.

Forelimb long, moderately slender; Fingers I equal to, or slightly longer than, Finger II; fingers unwebbed, lacking lateral fringes; Finger III not swollen in males; terminal

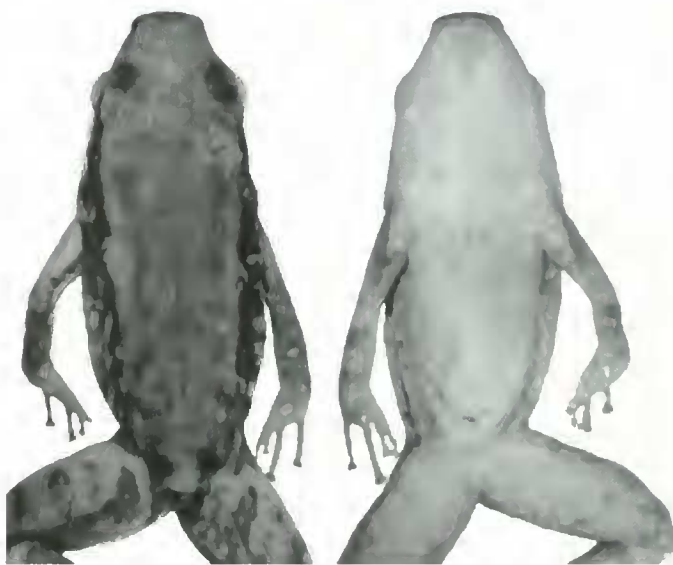


Fig. 14. *Colostethus utubambensis*, MHNSM 13990, female, 25.3 mm SVL.

discs slightly expanded, half again as wide as penultimate phalanges; subarticular tubercles large, rounded; supernumerary tubercles absent; palmar tubercle large, rounded; thenar tubercle smaller, ovoid; nuptial excrescences absent. Hind limb short, robust; tibia length 43.9–46.1% (\bar{x} = 45.0) SVL; foot length 41.9–44.0% (\bar{x} = 42.7) SVL; outer tarsal fold absent; inner tarsal fold shallowly sigmoid on distal half of tarsus, originating at elliptical inner tarsal tubercle; inner metatarsal tubercle large, ovoid; outer metatarsal tubercle smaller, rounded; toes webbed basally, lacking lateral fringes; terminal discs expanded, about half again width of penultimate segments; subarticular tubercles small, round; supernumerary tubercles absent.

Skin on dorsum and flanks finely shagreen; skin on ventral surfaces smooth; cloacal opening directed posteriorly at upper level of thighs; cloacal sheath short. Tongue, widest posteriorly, not notched, free behind for about half of its length; median lingual process absent.

Color in preservative Dorsum of head and body brown with nearly round, dark brown spots (Fig. 13); dark brown stripe across tip of snout extending through loreal and supratympanic regions and continuous with dark brown flanks; scattered, small, creamy white spots on lower parts of flanks; dorsolateral stripe broad, tan; oblique lateral stripe pale tan, extending from groin to anterior part of flank; ventrolateral stripe absent; upper lip and tympanic region cream. Forelimb pale tan with two dark brown, transverse bars on forearm and dark brown longitudinal stripe on anterior surface of upper arm; dorsal surfaces of hind limbs tan with dark brown transverse bars—four or five on thigh, four on shank, two on foot; anterior surface of thigh tan with longitudinal dark brown stripe; posterior surface of thigh

brown with small creamy white spots. All ventral surfaces creamy white, except plantar surfaces brown (Fig. 12).

Morales (1994) stated that the belly is gray in males and white in females; I noted no differences between the sexes 10 years after the description.

Color in life: Unknown.

Distribution and ecology.— This species is known only from the type locality in the valley of the Río Utcubamba, a tributary of the Río Marañón in northern Peru (Fig. 10)

Remarks.—Morales (1994:95) reported the type locality as “cerca de Tingo, Río Utcubamba, 2391 m.” My own altimeter readings at Tingo were 1810 m on 5 March 1979 and 1860 m on 24 January 1989, at which time I noted that the road follows the Río Utcubamba, which in many places is in a narrow canyon and quite picturesque. However, the hillsides have been cleared and the valley floor, what there is of it, is cultivated or in pasture. Below about 1900 m, columnar cacti are present, although at times of visits in January and March the area seemed to be quite wet.

In the diagnosis of this species, Morales (1994) stated that Fingers I and II were equal in length; in the description of the holotype, he stated that Finger I was shorter than Finger II, whereas in the illustration of the hand of the holotype, Finger I is notably longer than Finger II. Upon my request, Morales reexamined the holotype and reported (in litt., 14 February 2004) that Finger I is longer than Finger II.

The similarities of *Colostethus kingsburyi* and *C. utcubambensis* suggest that the two nominal taxa are either closely related or possibly conspecific. Rivero (1991b) noted variation in the anterior extent of the oblique lateral stripe and the presence or absence of a ventrolateral stripe. According to Coloma (1995), *C. kingsburyi* occurs in a narrow elevational belt of 1140–1300 m on the Amazonian slopes of the Andes in the Pastaza Trench and northward. Thus, a hiatus of about 550 km exists between the ranges of the two species. Until specimens become available from the intervening region or there is compelling evidence for their being conspecific, *C. utcubambensis* should be recognized as a distinct species. Likewise, preserved paratypes of *C. poecilonotus* and *C. utcubambensis* reveal only subtle differences between the species (e.g., dorsolateral stripe and basal webbing in *C. utcubambensis*).

Status of *Phyllobates peruvianus* Melin

Melin (1941) described *Phyllobates peruvianus* from Roque, Departamento de San Martín, Peru; the species was placed in *Colostethus* by Edwards (1971). The description was based on one male (NHMG 508) having a SVL of 21 mm and various characters mentioned by Melin (1941:61–62), “first finger about as long as second, Ö tympanum partly indistinct, about one-third diameter of the eye, Ö discs of fingers and toes fairly small, toes webbed at base.” Melin (1941:62) noted various aspects of the coloration in preservative: “a wedge-shaped blackish medial band on the back beginning at the eyes; another dark band from the nostril through the eye and above the tympanum towards the base of the forelimb, medially edged by a light band, continuing towards the base of the hind limb; sides of the upper jaw transversely banded; flanks blackish with light spots; limbs with diffuse cross bars; hinder part of the thighs blackish with light marble and dots; feet above light; body beneath whitish with a fine blackish mottle or dotting; hinder part of belly and thighs beneath whitish.” The “light band” extends from the orbit to the inguinal region and was defined as an oblique lateral stripe by Morales (1994), who examined the holotype and noted that dorsolateral and ventrolateral stripes were absent.

Roque is at an elevation of about 1200 m on the Amazonian slopes of the Cordillera Central in the Departamento de San Martín; thus, it is about midway between the type localities of *Colostethus idiomelus* and *C. mittermeieri* at Venceremos and the type localities of *C. craspedocephalus* and *C. sordidatus* at 30 km SW of Zapatero. *Colostethus mittermeieri* lacks pale stripes, and *C. craspedocephalus* and *idiomelus* have dorsolateral stripes and short or no oblique lateral stripes; furthermore, *C. craspedocephalus*, also differs from *C. peruvianus* by having Finger I longer than Finger II. *Colostethus sordidatus* is like *C. peruvianus* in having an oblique lateral stripe, no dorsolateral stripe, and Fingers I and II equal in length, but it differs from *C. peruvianus* in having the toes about three-fourths webbed, as contrasted to basal webbing in *C. peruvianus*. Furthermore, adult males of *C. sordidatus* have SVLs of 24.2–29.9 (\bar{x} = 25.7, N = 9) in contrast to 21 mm in the holotype of *C. peruvianus*, an adult male transporting tadpoles.

Thus, *Colostethus peruvianus* remains an enigma. Since the capture of the type specimen in 1925, no additional specimens have been found.

DISCUSSION

LIFE HISTORY AND TADPOLES

Like most other dendrobatid frogs, with the possible exception of *Aromobates*, members of the genus *Colostethus* typically deposit their eggs amidst leaf litter or soil on the forest floor; an exception is *C. beebei* which deposits eggs

on the leaves of terrestrial bromeliads (Bourne et al., 2001). Eggs usually are attended by males; upon hatching, the tadpoles wriggle onto the back of the attendant male, who transports them to water. However, egg attendance and transportation of tadpoles is by females in *C. inguinalis* and

C. pratti (Grant, 2004). Both sexes of *C. talamancae* have been reported to transport tadpoles (Breder, 1946; Silverstone 1976). Of six *Colostethus elachylistus* that were transporting tadpoles, one from Ayabaca, Departamento de Piura, is a gravid female and five from other localities are males. These limited data suggest that larval transport (and probably egg attendance) is amphisexual in *C. elachylistus*, or that the populations represented are different species.

The tadpoles of at least four species of *Colostethus* are nonfeeding; *C. chalcopis* on the island of Martinique, and *C. nidicola*, and *C. stepheni* in Amazonian Brazil are not transported; instead they are nidicolous and complete their development in terrestrial nests (Caldwell and Lima, 2003; Kaiser and Altig, 1994; Junc et al., 1994). The tadpoles of *C. degranvillei* also are nonfeeding and complete their development on the back of an attendant male (Claessen, 2002; Lescure, 1975).

Clutch size in species having transported, feeding tadpoles is 12–40 (Coloma, 1995; Lima et al., 2002; Lüddecke, 1999; Wells, 1980). Caldwell and Lima (2003) summarized data on clutch parameters in three nidicolous species of *Colostethus*; ovarian complements are 1–6, and diameter of ovarian eggs is 2.0–2.7 mm. The presence of only six unpigmented eggs about 2.0 mm in diameter in a female of *C. ornatus* in Peru indicates that this may be another nidicolous species.

Growth of back-riding tadpoles has been reported for *Colostethus subpunctatus* by Stebbins and Hendrickson (1959) and *C. panamensis* (as *C. inguinalis*) by Wells (1980). Back-riding tadpoles in 13 lots of six species (*Colostethus craspedocephus*, *elachylistus*, *eleutherodactylus*, *idiomelus*, *nexipus*, and *sylvaticus*) are in Stages 24 or 25; these tadpoles range in body length from 3.3–4.9 mm and in total length from 8.7–17.4 mm. The smallest back riding tadpoles have an undifferentiated gut, and the body cavity is filled with yolk; larger tadpoles have coiled intestines and commonly still contain yolk. The normal sequence of ontogenetic development of labial tooth rows in anurans is 1/0, 1/1, 1/2, 2/2, 2/3 (Altig and McDiarmid, 1999). The smallest tadpoles of *C. elachylistus*, *idiomelus*, and *nexipus* have LTRFs of 0/0. In *C. elachylistus*, *eleutherodactylus*, and *nexipus*, the ontogenetic sequence in LTRF in back-riding tadpoles is 0/0, 1/0, 1/1, 2/1, 2/2. (See species accounts and Table 3.) The full complement of labial teeth (2/3) apparently is not developed until the tadpoles become free swimming. In contrast, the ontogenetic sequence in back-riding tadpoles of *C. idiomelus* is 0/1, 0/1, 0/2, 0/3; all free-swimming tadpoles have an LTRF of 2/3. Neither of these sequences is like the “normal” sequence stated by Altig and McDiarmid (1999). It is unclear why tadpoles of *Colostethus* should differ in the ontogenetic sequence of tooth-row development.

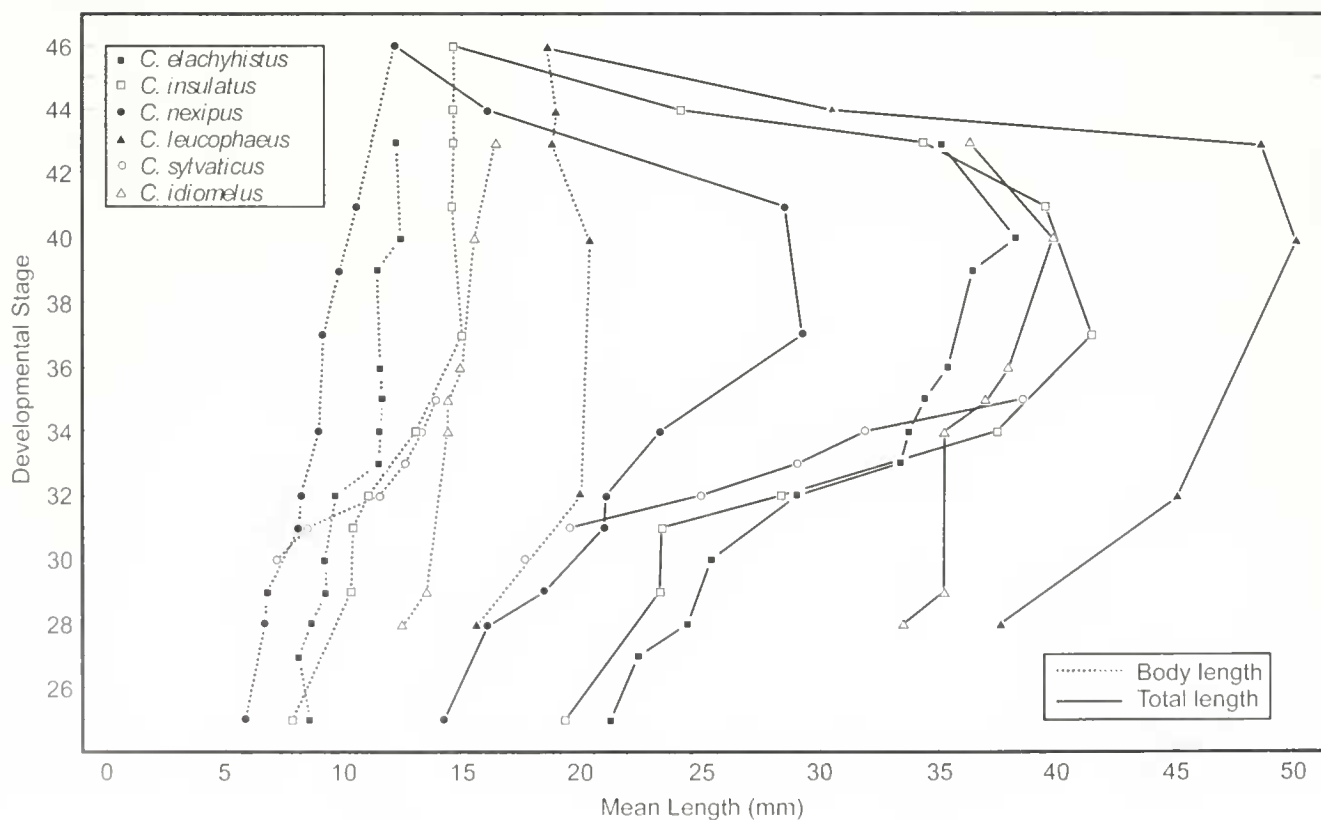


Fig. 15. Growth trajectories of tadpoles of six species of *Colostethus*.

Tadpoles of *Colostethus* in the Andes of northern Peru described herein are rather nondescript larvae; all taxa are similar in general shape and proportions, and none has distinctive coloration (Fig. 9). The largest tadpoles are those of *C. leucophaeus* with a body length of 20.5 mm and a total length of 50.2 mm (Stage 40); the smallest are those of *C. nexipus* with a body length of 10.3 mm and a total length of 28.2 mm (Stage 41). This is apparent in the growth trajectories of the two species; the tadpoles of other species are intermediate in their growth trajectories (Fig. 15).

ECOLOGY

Most species of *Colostethus* are active by day in and along small streams. The nature of the streams differs among some species. *Colostethus idiomelus* and *C. leucophaeus* were found in marshy streams or spring seepages, and *C. mittermeieri* was in a small mossy stream flowing from a nearby spring. *Colostethus aeruginosus*, *craspedocephus*, *insulatus*, *nexipus*, *pulcherrimus*, *sordidatus*, and *sylvaticus* were found only in rocky streams, and *C. elachyhistus* occurs in rocky streams and irrigation ditches. *Colostethus eleutherodactylus*, *ornatus*, and *spilotogaster* were found in areas of leaf litter on the forest floor. No ecological data are available for *C. argyrogaster*, *pocilonotus*, and *utubambensis*.

Only seven instances of sympatry are documented among *Colostethus* in the Andes of northern Peru (Fig. 16), and for the locality 20 km south of Chiriaco, no ecological data are available. With the exception of the locality 16 km ESE of Shapaya, significant differences in snout-vent length exist between the sympatric species. At the exception, *C. nexipus* inhabits streams, whereas *C. eleutherodactylus* was found on the forest floor litter. Also, at Ponga de Shilcayo, *C. nexipus* inhabits the stream, whereas *C. ornatus* was found on the forest floor litter. However, Coloma (1995) noted that five *C. nexipus* were under pieces of wood inside a house close to a swampy area in Limón, Ecuador; other Ecuadorian specimens were from streams. At the rocky ravine 30 km SW of Zapatero, the small *C. craspedocephus* was active on small boulders in the stream by day when individuals of the larger *C. sordidatus* were found only under stones at the edge of the stream. However, at night, *C. sordidatus* were perched on the boulders in the stream, and no *C. craspedocephus* were observed.

Tadpoles of *Colostethus* primarily inhabit quiet pools in streams. At least in two cases, tadpoles of sympatric species differ slightly in size. On the western slope of the Cordillera de Huancabamba, tadpoles of *C. elachyhistus* in Stage 35 have total lengths of 32.7–36.6 mm (\bar{x} = 34.58), whereas those of *C. sylvaticus* in Stage 35 have total lengths of 38.1–39.3 mm (\bar{x} = 38.56). Likewise, at 30 km SW of

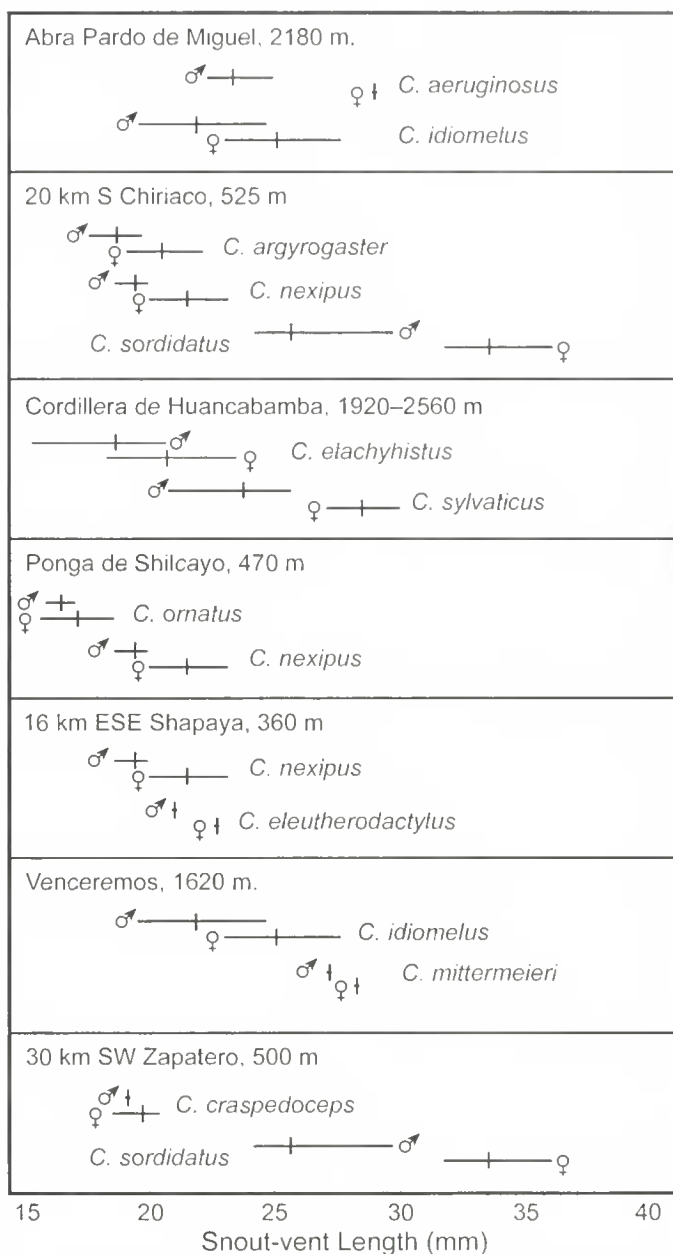


Fig. 16. Sizes of sympatric species of *Colostethus* at seven localities in northern Peru. Horizontal lines are ranges and vertical lines are means.

Zapatero, tadpoles of *C. craspedocephus* in Stage 25 have total lengths of 15.9–23.7 mm (\bar{x} = 20.68), and those of *C. sordidatus* in the same stage have total lengths of 19.4–33.5 mm (\bar{x} = 26.44).

These few observations and limited data suggest that sympatric species of *Colostethus* may differ in (1) size of adults, (2) size of tadpoles, (3) microhabitat, or (4) time of activity. Obviously, these possibilities need to be examined in detail.

table 12. Geographic and elevational distribution of species of *Colostethus* in northern Peru. Numbers are elevations in meters.

Species	Cordillera Occidental	Cordillera Colán	Cordillera de Huancabamba	Marañón Valley	Cordillera Central	Eastern Foothills
<i>C. aeruginosus</i>	—	—	—	—	1980–2180	—
<i>C. argyrogaster</i>	—	—	—	525–550	—	500–600
<i>C. craspedocephalus</i>	—	—	—	—	—	500
<i>C. elachyhistus</i>	725–2760	—	710–2590	—	—	—
<i>C. eleutherodactylus</i>	—	—	—	—	—	360
<i>C. idiomelus</i>	—	—	—	—	1620–2840	—
<i>C. insulatus</i>	—	—	—	1260–2600	—	—
<i>C. leucophaeus</i>	—	—	—	—	2400	—
<i>C. mittermeieri</i>	—	—	—	—	1620–2050	—
<i>C. nexipus</i>	—	—	—	—	325–810	360
<i>C. ornatus</i>	—	—	—	—	470–680	350
<i>C. poecilonotus</i>	—	—	—	500	—	—
<i>C. pulcherrimus</i>	2620	—	—	—	—	—
<i>C. sordidatus</i>	—	—	—	—	520	500
<i>C. spilotogaster</i>	—	2325	—	—	—	—
<i>C. sylvaticus</i>	2460	—	1920–3100	—	—	—
<i>C. utcubambensis</i>	—	—	—	1845	—	—

BIOGEOGRAPHY

With the exception of *Colostethus elachyhistus*, *idiomelus*, and *sylvaticus*, each species of *Colostethus* in the Andes of northern Peru is known from few localities and six species (*C. craspedocephalus*, *eleutherodactylus*, *leucophaeus*, *poecilonotus*, *pulcherrimus*, and *spilotogaster*) are known from a single locality. Consequently, no biogeographic synthesis is possible. However, existing data indicate a general picture of geographic and elevational distribution (Table 12; Fig. 14).

The greatest diversity of *Colostethus* in northern Peru is in the Cordillera Central and associated ranges to the east of the Río Mayo. This region contains the wettest environments that are mainly developed on the eastern slopes of the mountains. Of the nine species known from this region, two (*C. craspedocephalus* and *C. eleutherodactylus*) apparently are restricted to elevations of less than 500 m at the base of the mountains. Two others (*C. argyrogaster* and *C. sordidatus*) occupy the same elevational range at the eastern base of the mountains, and *C. nexipus* has a greater elevational range (520–810 m). These three species also occur at elevations of about 500 m on the drier western slopes of the Cordillera Oriental. If there is, or has been, a continuity in their distributions, presumably it is around the northern end of the Cordillera Central and not across the high elevations of the cordillera.

The other four species in the Cordillera Central are restricted to higher elevations in the cordillera; *Colostethus idiomelus* and *C. mittermeieri* descend to 1620 m on the eastern slopes of the Cordillera Central. The former also ranges westward in the Cordillera. *Colostethus aeruginosus* is known only from high elevations (1980–2180 m) on the humid eastern slopes, whereas *C. leucophaeus* is known only

from 2400 m in the highlands. One species, *C. spilotogaster*, is known from an elevation of 2325 m in the Cordillera Colán, a northern extension of the Cordillera Central.

In contrast to the Cordillera Central, only three species of *Colostethus* are known from the Cordillera Occidental and its associated ranges (Cordillera de Cuchallí, Cordillera de Huancabamba, and Cordillera de Tabacónas). *Colostethus elachyhistus* is widespread geographically (Fig. 9) and is known from elevations of 725–2590 m. *Colostethus sylvaticus* is more restricted geographically at elevations of 1920–3100 m, whereas *C. pulcherrimus* is known from a single locality at 2620 m. Except for isolated areas at higher elevations, the western slopes of the Cordillera Occidental are dry with few permanent streams; consequently, these slopes lack the diversity of *Colostethus* that is evident on the humid eastern slopes of the Cordillera Central. *Colostethus elachyhistus* occurs on the high (2020 m) Pacific slopes and eastern slopes of the Abra de Porculla, the lowest pass in the Cordillera Occidental, and at 2500 m in the upper valley of the Río Requena.

Most areas in the arid valley of the Río Marañón seem to be uninhabitable by *Colostethus*, but numerous small streams that plunge down the western slopes of the Cordillera Central and eastern slopes of the Cordillera Occidental provide adequate habitat for these frogs. Three species (*C. insulatus*, *poecilonotus*, and *utcubambensis*) are known only from these tributaries to the Río Marañón. As noted previously, three other species (*C. argyrogaster*, *nexipus*, and *sordidatus*) that occur in the eastern foothills of the Cordillera Central presumably entered the more northern part of the Río Marañón Valley around the northern end of the Cordillera Central.

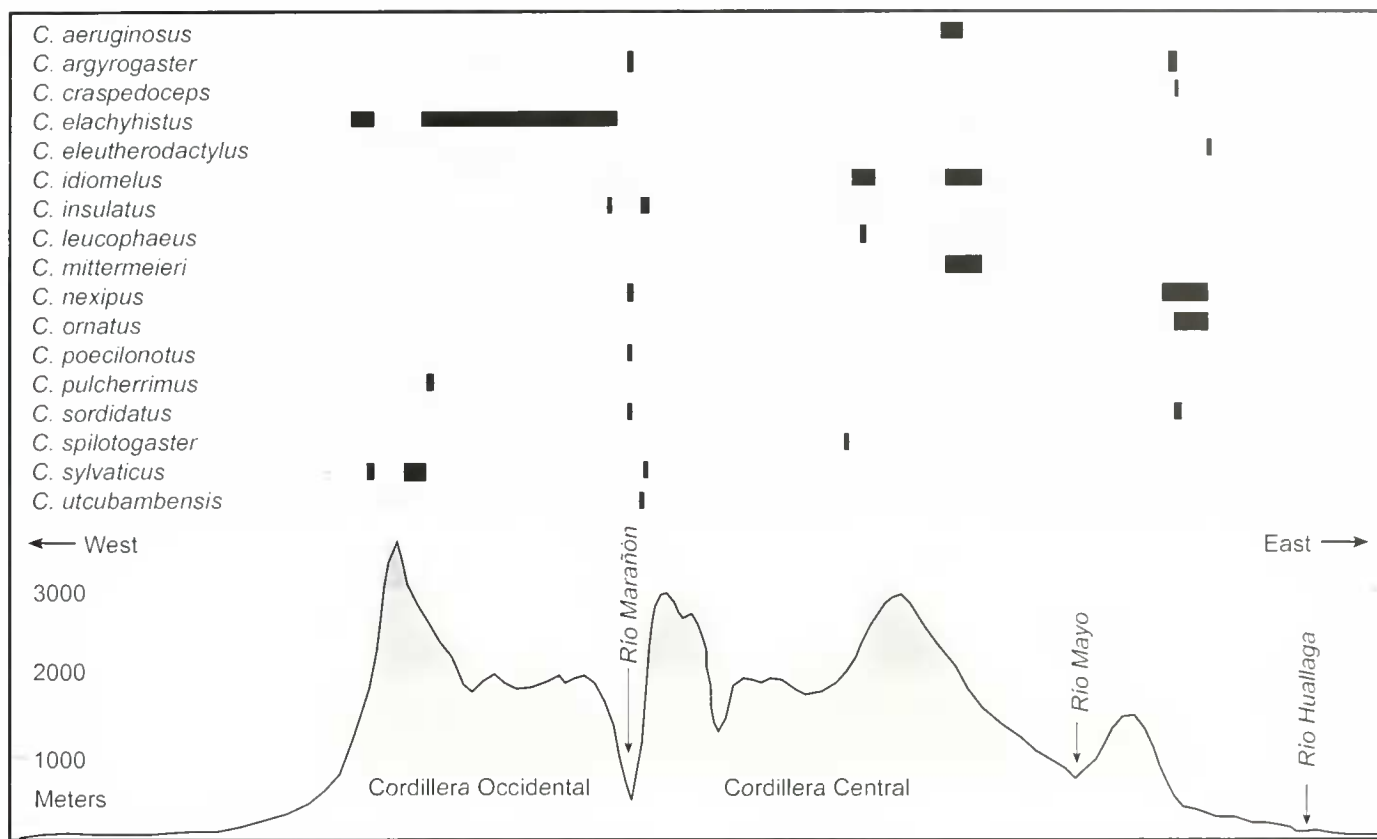


Fig. 17. Profile of the Andes at about 6° S Lat. in northern Peru; vertical exaggeration is about 35X. Black bars indicate distributions of species of *Colostethus*. The ranges of *C. spilotogaster* and *C. sylvaticus* are at about 5°30'.

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APPENDIX I

SPECIMENS AND LOCALITIES

The specimens from the Andes of northern Peru and comparative material of the same species from Ecuador are documented below, alphabetically by species. Localities are arranged alphabetically within departamentos or provincias, which also are arranged alphabetically within countries. Within a locality, specimens are listed chronologically by catalogue number following museum abbreviations, which are arranged alphabetically.

Colostethus acrimosus

PERU: *San Martín*. East slope of Abra Pardo de Miguel. Provincia Rioja, 1980–2180 m, KU 211940 (holotype), 211941–43, 211945, MHNSM 6225–27.

Colostethus argurogaster

PERU: *Amazonas*. 20 km SW Chiriaco, 525 m. Provincia de Bagua Grande, KU 196717, I SUMNS 32523; Imaz, Provincia de Bagua Grande, MHNSM 14256 (holotype), 14257–58. *San Martín*. 33 km NNE (by road) of Tarapoto, Provincia de San Martín, MHNSM 1801–14, 2815–16 (C&S); 26–27 km NNE of Tarapoto, Provincia de San Martín, MHNSM 14805–07.

Colostethus craspediceps

PERU: *San Martín*. 30 km SW of Zapatero (10 km NE of San José de Sisa), 500 m, Provincia de Lamas, KU 211952 (holotype), 211953–59, 215609–10 (tadpoles).

Colostethus elachylustus

ECUADOR: *Loma*. 2 km NE Sabiango, 850 m, KU 142531; 17 km NE Macara, 1240 m, KU 142613–30; 5 km NE Carimanga, 1870 m, KU

142532–43, 142507–17; Loja, 2150 m, KU 120515–20, 120522–39, 120540 (holotype), 120542 (C&S); 2 km N Loja, 2100 m, KU 142351–76; 4 km S Loja, 2180 m, KU 142344–49; 7.6 km S Loja, 2210 m, KU 142350; 14.4 km S Loja, 2260 m, KU 202820–21; 12 km S Loja, 2250 m, KU 166091–98; 3 km W Loja, 2150 m, KU 138800–08; 5.2 km W Loja, 2130 m, KU 202816–17, 202618–19 (C&S); 10 km W Loja, 2500 m, KU 138810; 2.7 km N San Lucas, 2620 m, KU 182110–11, 182112 (C&S), 182113–17; 6 km N San Lucas, 2760 m, KU 166099.

PERU: *Cajamarca*: 1 km S Cajabamba, Provincia de Cajabamba, 2650 m, KU 211846–52, 212490 (tadpoles), MHNSM 6252–56; Cutervo, Provincia de Cutervo, 2620 m, KU 211843–45, MHNSM 6250; 4 km W Llama, Provincia de Chota, 2500 m, KU 212518–24, 212489 (tadpoles), MHNSM 6246–48, 6298 (tadpoles); 28 km N Santa Cruz, 725 m, KU 196710–16, LSUMNS 18566–67. *Piura*: Ayabaca, Provincia de Ayabaca, 2750 m, KU 212510–17, 212487–88 (tadpoles), MHNSM 6241–45, 6297 (tadpoles); NE slope Abra de Porculla, 2080 m, KU 163094–110 164038–40 (tadpoles); NE slope Abra de Porculla, 2200 m, KU 212505–09, MHNSM 6236–40; SW slope Abra de Porculla, 1580 m, KU 163123; 164044 (tadpoles); SW slope Abra de Porculla, 1850 m, KU 163111–22 164042–43 (tadpoles); SW slope Abra de Porculla, 2020 m, KU 164041 (tadpoles); Canchaque, 1300 m, KU 138758 (tadpoles), 138811–12, 219750–52, 219753 (tadpoles), MHNSM 15382 (tadpoles); 5 km E Canchaque, 710 m, LSUMNS 32532; 12 km E Canchaque, 1770 m, KU 181643, 181866 (tadpoles); 15 km E Canchaque, 1760 m, LSUMNS 32508–18; 17.7 km E Canchaque, 1920 m, UF 52043–46, 106988–7022; 21 km E Canchaque, 2070 m, UF 52139–40; 24 km E Canchaque, 2240 m, UF 107023; 30 km E Canchaque, 2530 m, UF 52145–46; 30.6 km E Canchaque, 2590 m, UF 106980–87; 8.5 km W Canchaque, 620 m, KU 219745–49, 219754 (tadpoles); Huancabamba, 1900 m, KU 138062–70, 138763 (tadpoles), 181644–51 181867 (tadpoles); 4 km SW Huancabamba, 1980 m, KU 181652–66, 181867.

Colostethus cleutherodactylus

PERU: *San Martín*: 16 km ESE Shapaja, 360 m, Provincia de San Martín, KU 211813, 211814 (holotype)

Colostethus idiomelus

PERU: *Amazonas*: 2 km E Balzapata, 2220 m, Provincia de Bongará, KU 211891–905, MHNSM 6231–35; 8 km NNE Balzapata, 1850 m, Provincia de Bongará, KU 181680; 12 km NNE Balzapata, 1940 m, KU 211890, 215604 (tadpoles), MHNSM 6223–24; 11 km SSE Chachapoyas, 2840 m, Provincia de Chachapoyas, KU 211884; Pomacochas, 2150 m, Provincia de Bongará, KU 181681–99, 181871–72 (tadpoles), 211885–89, 215605 (tadpoles), MHNSM 6228–30, 6272 (tadpoles); 5 km W Pomacochas, 2228 m, LSU 19576–83. *San Martín*: East slope Abra Pardo de Miguel, 1980 m, Provincia Rioja, KU 215608 (tadpoles); East slope Abra Pardo de Miguel, 2180 m, Provincia Rioja, KU 211906–39, 215606–07 (tadpoles); Venceremos, 1620 m, Provincia Rioja, MCZ A-100260 (Holotype).

Colostethus insulatus

PERU: *Amazonas*: 16 km ENE Balsas, Provincia Chachapoyas, 1650 m, UF 37536–41; 17 km ENE Balsas, Provincia Chachapoyas, 1810 m, KU 211857 (holotype) 211858–70, 211560 (tadpoles), MHNSM 6206–14, 6274 (tadpoles); 24 km ENE Balsas, Provincia Chachapoyas, 2160 m, KU 211871–72; 37 km ENE Balsas, Provincia Chachapoyas, 2600 m, KU 211873–74; 33 km SE Ingenio, 1850 m, LSU 32548–51; 6 km W Pedro Ruiz, Provincia Bongará, 1260 m, KU 211875–78, 215601 (young), 215602 (tadpoles), MHNSM 6219–21, 6269 (tadpoles), 6284 (young). *Cajamarca*: 11 km W Balsas, Provincia Celendín, 1600 m, KU 211853–56, 215599 (tadpoles), MHNSM 6266–68, 6276 (tadpoles); 2 km NW San Juan, 2290 m, KU 211833–42, 215598 (young), MHNSM 6257–65.

Colostethus leucophaeus

PERU: *Amazonas*: Molinapampa, Provincia Chachapoyas, 2400 m, KU 211879 (holotype), 211880–83, 215603 (tadpoles), MHNSM 6215–17, 6271 (tadpoles).

Colostethus nattermeieri

PERU: *San Martín*: East slope Abra Pardo de Miguel, 2050 m, Provincia Rioja, KU 211944; Venceremos, Provincia Rioja, 1620 m, MCZ A-100217 (holotype), MCZ A-100218–57.

Colostethus nexipus

ECUADOR: *Morona Santiago*: 5.3 km NE Plan de Milagro, 2550 m, KU 202822–24; Méndez, 500 M, KU 220664; Limón, 1090 m, KU 220661–63; Los Tayos, KU 194164.

PERU: *Amazonas*: 43 km NE Chiraco, 325 m, LSUMNS 53430; 20 km SW Chiraco, 520 m, KU 196727–28, 196730; LSUMNS 32547. *San Martín*: Cataratas Ahuashiyacu, 14 km NE Tarapoto, Provincia de San Martín, 730 m, KU 211805–10, MHNSM 6200–05; cordillera NE of Tarapoto, Provincia de San Martín, 600 m, KU 209397–98; Ponga de Shilcayo, 4 km NNW Tarapoto, Provincia de San Martín, 470 m, KU 211830; 6 km ESE Shapaja, Provincia de San Martín, 310 m, KU 212486 (tadpoles); 14 km ESE Shapaja, Provincia de San Martín, 360 m, KU 211815–29, KU 215594 (tadpoles); 15 km ESE Shapaja, Provincia de San Martín, 360 m, KU 211811–12; 16 km ESE Shapaja, Provincia de San Martín, 360 m, KU 215593; 17 km NE Tarapoto, Provincia de San Martín, 850 m, MHNSM 6199; 22.7 km NE Tarapoto, Provincia de San Martín, 810 m, KU 211831; 215596 (tadpoles); 23.2 km NE Tarapoto, Provincia de San Martín, 800 m, KU 215595; 28 km NE Tarapoto, Provincia de San Martín, 600 m, KU 211832.

Colostethus ornatus

PERU: *San Martín*: Ponga de Shilcayo, about 4 km NNW of Tarapoto, Provincia de San Martín, 470 m, KU 211950. Tarapoto, Provincia de San Martín, 350 m, MHNSM 17713–17.

Colostethus peruvianus

PERU: *San Martín*: Roque, NHMG 508 (holotype).

Colostethus poecilonotus

PERU: *Amazonas*: Alva, 500 m, MCZ A-89106–07 A-89108 (holotype), A-89109.

Colostethus pulcherrimus

PERU: *Cajamarca*: Cutervo, Provincia de Cutervo, 2620 m, KU 211946 (holotype), 211947–49, MHNSM 6251.

Colostethus sordidatus

PERU: *Amazonas*: 20 km SW Chiraco, 520 m, Provincia de Bagua, KU 196718–26. *San Martín*: 30 km SW of Zapatero (10 km NE of San José de Sisa), 500 m, Provincia de Lamas, KU 211960 (holotype), 211961–72, 215611 (tadpoles).

Colostethus spilotogaster

PERU: *Amazonas*: Cordillera Colán, SE La Peca, 2326 m, LSUMNS 39341 (holotype).

Colostethus sylvaticus

PERU: *Cajamarca*: Tabacónas, Provincia de San Ignacio, MCZ 5344 (holotype), 5346, 5350, 5355–56. *Piura*: 17.7 km E Canchaque, 1920 m, UF 112484–89; 21 km E Canchaque, 2070 m, UF 112458; 24 km E Canchaque,

2240 m, UF 112494–98; 30 km E Canchaque, 2530 m, UF 52040–42, 112499–510; 30.6 km E. Canchaque, 2590 m, UF 52141–44, 112490–93; 12.7 km E El Tambo, 2820 m, KU 219756–58; 1 km W El Tambo, 2740 m, KU 219755; 15.5 km SW Huancabamba, 2560 m; 181670 (tadpoles); 25.5 km SW Huancabamba, 3010 m, KU 181668–73, 181868–69 (tadpoles); 29.3 km SW Huancabamba, 3010 m, KU 181667; 31 km SSW Huancabamba,

3080 m, KU 181674–79; summit of cordillera between Canchaque and Huancabamba, 3100 m, KU 138071–79.

Colostethus utubambensis

PERU: Amazonas: Tingo, MHNSM 13986 (holotype), 13987–91.

APPENDIX 2

GAZETTEER

Following is a list of localities in the Andes and adjacent lowlands of northern Peru where specimens of *Colostethus* were collected. After each place name the departamento is given in parentheses, followed by geographic coordinates, elevation and vegetation type. Coordinates were determined from maps (Mapa Físico Político del Perú, 1:1,000,000, 1973, and Carta Nacional del Perú, 1:100,000, 1986. Elevations were obtained from altimeter readings or from maps. When known, specific sites and habitats are given followed by names of collectors (only those responsible for field notes) and the months and years that they collected at the sites. Names of collectors are abbreviated: ERW = Erik R. Wild, GKN = G. K. Noble, LSU = Louisiana State University ornithologists, RAM = Russell A. Mittermeier, RS = Ranier Schulte, RT = Richard Thomas, THF = Thomas H. Fritts, WED = William E. Duellman. All localities are shown on the political map (Fig. 1).

Abra de Porculla (Piura)—05° 50' S, 79° 30' W, 2145 m; humid montane forest. Pass in the northern part of the Cordillera Occidental. Collections made on southwestern slope (2020 m) and northeastern slope (2080 m) in March 1975 by WED.

Abra Pardo de Miguel (Amazonas-San Martín)—05° 46' S, 77° 42' W, 2210 m; very humid montane forest. A pass in the eastern range of the Cordillera Central. Collections made on the east slope just below the crest on the road to La Rioja at an elevation of 2180 m and farther down the slope at 1980 m in January 1989 by WED.

Alva (Amazonas)—05° 53' S, 78° 56' W, 1000 m; presumably thorn forest. Site on slopes of Cordillera Central above Pedro Ruiz Gallo in Río Utcubamba Valley. Collection in May 1974 by RAM.

Ayabaca (Piura)—04° 38' S, 79° 43' W, 2750 m; mostly cutover humid montane forest. A small town in the northernmost part of the Cordillera Occidental in Peru. Collections made in the vicinity of the town in February 1989 by WED.

Balsas (Amazonas)—06° 50' S, 77° 59' W, 1090 m; thorn forest. A village in the narrow, subhumid Marañón Valley. Collections made at small streams and waterfalls at elevations of 1810, 2160, and 2600 m along the road ascending the western face of the Cordillera Central toward Chachapoyas in January 1989 by WED.

Balzapata (Amazonas)—05° 46' S, 77° 51' W, 1640 m. A village just west of the crest of the Cordillera Central. Collections made in disturbed and partly cutover humid forest 8 km NNE (1850 m) on the road to La Rioja in March 1979 by WED and at 2 km E (2200 m) and 12 km NNE (1940 m) in January 1989 by WED.

Cajabamba (Cajamarca)—07° 36' S, 78° 02' W, 2700 m; montane dry forest. Town in the Cordillera Central. Collections made in April 1970 by THF and in at 1 km south (2650 m) in March 1989 by WED.

Canchaque (Piura)—05° 22' S, 79° 36' W, 1120 m; tropical dry forest. A town near the western base of the Cordillera de Huancabamba. Collections were made in dry forest at Canchaque in May 1970 by THF and in March 1979 by WED, 5 km W (710 m) in December 1978 by RT, 6.5 km west (620 m) in January 1991 by ERW, in humid montane forest 12 km

east (1770 m) on the road to Huancabamba in March 1979 by WED, and 15 km east in December 1978 by RT.

Cataratas Ahuashuyacu (San Martín)—06° 30' S, 76° 20' W, 730 m; humid subtropical forest. Waterfall and rocky stream in deep ravine 14 km NNE of Tarapoto on the road to Yurimaguas. Collections in February 1989 by WED.

Chachapoyas (Amazonas)—06° 13' S, 77° 50' W, 2360 m; disturbed humid montane forest. Town in the Cordillera Central. Collections made in humid montane forest at an elevation of 2340 m 11 km SE of town in January 1989 by WED.

Chiriaco (Amazonas)—05° 09' S, 78° 21' W, ±450 m; thorn forest. Town on the Río Marañón at the confluence of the Río Chiriaco. Collections made in dry forests at 43 km NE in October 1978 by LSU and at 4 km SW and 20 km SW (525 m) on the road to Bagua in December 1974 by RT.

Cutervo (Cajamarca)—06° 22' S, 78° 49' W, 2620 m; cultivated valley in the northern part of the Cordillera Occidental. Collection in February 1989 by WED.

El Tambo (Piura)—05° 21' S, 79° 33' W, 2770 m; humid montane forest. Settlement on the western slope of the Cordillera de Huancabamba, 31 km NNE of Canchaque on the road to Huancabamba. Collections in relatively undisturbed forest at 1 km W (2740 m) and 12.7 km E (2820) in January 1991 by ERW.

Huancabamba (Piura)—05° 14' S, 79° 28' W, 1900 m; dry forest. Town on the Río Huancabamba at eastern base of the Cordillera de Huancabamba; area in immediate vicinity mostly cultivated. Collections made in town and at summit of Cordillera de Huancabamba (3100 m) in May 1970 by THF and in humid montane forest at 4 km SW (1980 m), 15.5 km SW (2560 m), 25.5 km SW (3010 m), 29.3 km SW (3010 m) and 31 km SW (3080 m) on the road to Canchaque in March 1979 by WED.

Imaza (Amazonas)—Morales and Schulte (1994) gave approximate coordinates of 04° 15' S, 78° 20' in "Bagua Grande, Amazonas." These coordinates are well within Provincia Condorcanqui; no place name of Imaza could be found in that region. The Río Imaza is at approximately 05° 16' S, 78° 17' W in Provincia Bagua, Departamento Amazonas. Both sites are within the Marañón Valley. April 1990 by Padre Pedro Cashiro.

Ingenio (Amazonas)—05° 55' S, 78° 55' W, 1280 m; thorn forest. Settlement in the Río Utcubamba Valley. Collection from dry forest on slopes of Cordillera Central 33 km SE (1830 m) on road to Pomacochas in December 1974 by RT.

Lamas (Llama) (Cajamarca)—06° 31' S, 70° 07' W, ±2200 m; thorn forest. Village in valley on west slope of Cordillera Occidental. Collection from roadside ditch 4 km W (2500 m) in March 1989 by WED.

La Peca (Amazonas)—05° 36' S, 78° 22' W, ±1400 m; thorn forest. Village near western base of the Cordillera Colán. Collection from humid montane forest SE of village at 2625 m in October 1978 by LSU.

Molunapampa (Amazonas)—06° 11' S, 77° 38' W, 2400 m; mostly cultivated montane dry forest. A small town in the upper Río Utcubamba Valley. Collection in vicinity of town in January 1989 by WED.

Pedro Ruiz Gallo (Amazonas)—05° 25' S, 77° 57' W, 1280 m; thorn forest. Small village in the middle Río Marañón Valley. Collection from small stream 6 km W (1260 m) on road to Bagua in January 1989 by WED.

Pomacochas (= Florida) (Amazonas)—05° 49' S, 77° 55' W, 2150 m; mostly cultivated humid montane forest. Village in northern part of Cordillera Central. Collections from vicinity of village in March 1979 and January 1989 by WED, and 5 km west (2228 m) in July 1968 by RT.

Ponga de Shulcano (San Martín)—06° 31' S, 76° 53' W, 470 m; humid tropical forest. Deep ravine 4 km NNW of Tarapoto. Collection in February 1989 by WED.

Río Cumbaza Valley (San Martín)—06°29' S, 76°23' W, 430 m; tropical forest. Shallow, narrow valley of a tributary of the Río Mayo. Collection made in February 1989 by WED.

Roque (San Martín)—06°24' S, 76°48' W, ±1200 m; humid montane forest. Village on the Amazonian slopes of the northern part of the Cordillera Central. Collection made in 1923 by Douglas Melin.

San Andrés de Cutervo (Cajamarca)—06°14' S, 78°43' W, 2850 m; dry montane forest. Village in northern part of Cordillera Occidental. Collection from cave near village.

San Juan (Cajamarca)—07°15' S, 78°30' W, 2290 m; montane dry forest. Town in the upper Río Magdalena Valley on the west slope of the Cordillera Occidental. Collection from 2 km N on road to Cajamarca in January 1989 by WED.

Santa Cruz (Cajamarca)—06°05' S, 78°51' W, ±1300 m; thorn forest. Village in the Río Chamaya Basin. Collection from 28 km N (725 m) in December 1974 by RT.

Shapaja (San Martín)—06°36' S, 76°17' W, 310 m; mostly cutover humid tropical forest. Village just north of the Río Huallaga. Collections

made at 6 km ESE (310 m) and 14–16 km ESE (360 m) on the road to Chazuta in February 1989 by WED.

Tabacónas (Cajamarca)—05°19' S, 79°17' W, ±2000 m; humid tropical forest. Village in Cordillera de Tabacónas. Collection made in September 1916 by GKN.

Tarapoto (San Martín)—06°31' S, 76°23' W, 370 m; humid tropical forest. Town near the confluence of the Río Mayo and Río Huallaga just east of the Cordillera Central. Collections made in outlying ridge of the Andes at 12 km NE (720 m), 22.7 km NE (810 m), 23.2 km NE (800 m), 28 km NE (600 m) on the road to Yurimaguas in February 1989 by WED.

Tingo Amazonas—06°21' S, 77°49' W, 1835 m; cultivated dry forest. Village on Río Utcubamba. Collection made in November 1980 by RS.

Venceremos (San Martín)—05°44' S, 77°31' W, 1630 m; humid montane forest. Former road camp and now small settlement on the road between Balzapata and La Rioja. Collection made in September 1978 by RAM.

Zapatero (San Martín)—06°34' S, 76°30' W, 320 m; humid tropical forest. Village at base of hills north of the Río Huallaga. Collections from ravine in cutover humid tropical forest at 30 km SW (500 m) in February 1989 by WED.